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Flammulated, Boreal, and Great Gray Owls in the United States:

A Technical Conservation Assessment

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Abstract

Flammulated (*Otus flammeolus*), boreal (*Aegolius funereus*), and great gray (*Strix nebulosa*) owls occur over a broad portion of North America and each is designated as a "sensitive species" in four or more USDA Forest Service regions. The insectivorous **flammulated owl** is a neotropical migrant requiring suitable wintering habitat in the extreme southwestern United States, Mexico, and Central America as well as breeding habitat in the mountains of the western United States. Flammulated owls breed predominantly in yellow-pine (*Pinus ponderosa* and *Pinus jeffreyi*) forests and are cavity nesters. The mature and older ponderosa pine forests used as breeding habitat by flammulated owls have changed during the past century due to fire management and timber harvest. In contrast, the **boreal owl** is a nomadic, small mammal specialist that occurs as an "island" species occupying subalpine and boreal forests. Movements among populations are probably important to boreal owl persistence, and coordinated management of disjunct populations in different Forest Service regions may be important. While the boreal owl's high altitude spruce-fir forests have remained relatively undisturbed in the past, they are coming under increasing harvest pressure as the stock of lower elevation older stands are depleted or reserved. **Great gray owls** in the western United States occur in mid to high elevation conifer forests. These owls usually nest in mature and older forest stands using existing raptor nests or tops of broken trees and snags for a nest platform. The species' requirement of a secure nesting platform leads to one potential ecological limitation on population size. Prey availability is the other factor thought to limit populations. Flammulated and boreal owls may face significant conservation problems in the absence of conservation planning. Both owls are associated with older forest habitats. Limited research on these species indicates that their demography and life history coupled with their fairly narrow habitat associations make them vulnerable to habitat change. Current forest management practices in many areas (i.e., stand replacement systems) remove quality habitat for these species. Therefore, on at least a local basis, persistence of these species could be in jeopardy, even in the short term. Long-term concerns are greater because the habitats that seem most important to these species require one to two centuries to regenerate. Furthermore, the population biology of both species necessitates across-region planning to facilitate effective conservation planning. Based on limited information, the persistence of great gray owl populations in the United States over both the short and long-term is more certain. Great gray owl foraging habitat use is more compatible with current forest management practices. Our understanding of the ecology and biology of these three species is not sufficient to produce a conclusive assessment of their conservation status. The enclosed assessments, however, give a sufficiently clear picture of each owl's status and the dynamics of important forest habitats to influence management and research decisions. It is clear that development of conservation strategies would aid management but current knowledge of these species is insufficient to produce such a specific document.

Keywords: flammulated owl, boreal owl, great gray owl, *Otus flammeolus*, *Aegolius funereus*, *Strix nebulosa*, habitat relationships, old growth, forest dynamics, ponderosa pine forest, spruce-fir forest, conservation.

Cover photos, clockwise starting in the upper left corner:

Adult great gray owl by Michael S. Quinton. Insert—juvenile great gray owl by James Duncan.
Adult flammulated owl by Richard T. Reynolds. Insert—juvenile flammulated owl by Richard T. Reynolds.
Adult boreal owl by Pat and Greg Hayward. Insert—juvenile boreal owl by Pat and Greg Hayward.

FLAMMULATED, BOREAL, AND GREAT GRAY OWLS IN THE UNITED STATES: A TECHNICAL CONSERVATION ASSESSMENT

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Part I: INTRODUCTION

Approach: The Flammulated, Boreal, and Great Gray Owl Assessments

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This forest owl conservation assessment focuses on three species of forest owls that occur on national forest lands in the United States. Sixteen other species of owls also regularly breed in the United States, but these three species were designated "sensitive" on forests in more than one region of the Forest Service in 1992. Within the National Forest System, "sensitive species" are plants and animals whose population viability is identified as a concern by a regional forester. Sensitive species require special management, so knowledge of their biology and ecology is critical. The inter-regional distribution of these owls necessitates a coordinated approach to management. Therefore, the forest owl conservation assessment addresses the biology of these owls throughout their range within the United States. The broad nature leads to some constraints on the specificity of information for particular locales. Furthermore, completing the assessments promptly required establishment of some sideboards concerning the geographic scope of particular aspects of the assessment and further analysis of existing (but unanalyzed) field data. These sideboards are described later in this introduction. This brief chapter outlines the scope of the assessments and describes the process used in producing the assessments.

GOALS

First, the authors sought to provide forest managers, research biologists, and the public with a thorough discussion of the biology, ecology, and conservation status of these forest owls based on scientific knowledge accumulated prior to March 1993. This discussion includes the authors' interpretation of the strength of scientific evidence for particular conclusions concerning the biology or ecology of the species. Second, the authors sought to provide an overview of research necessary to broaden current scientific knowledge before presenting scientifically based conservation strategies for the species.

The assessment goals explicitly limit the scope of this document to critical summaries of scientific

knowledge, discussion of broad implications of that knowledge, and outlines of information needs. As such, we do not provide management guidelines. The assessments are management tools in that they provide the biological basis for management. The assessments provide the catalyst to integrate research and management activities. The research direction outlined in each assessment is designed to meet specific management needs. Much of this research can be accomplished most effectively if undertaken as part of active management programs on national forest lands. For example, when researchers and managers work together, research can effectively address current management problems, and research can use the large-scale "treatments" that result from carefully planned management actions. Therefore, we felt that focusing the assessments on these goals would provide the information needed by both managers and researchers to move toward developing a conservation strategy for these species in the shortest possible time.

SCOPE OF ASSESSMENT

The forest owl conservation assessment consists of three major sections (individual owl assessments), each designed to stand alone. The assessments were written from a common outline, however, to facilitate comparison of the scientific understanding of the three owls. Each conservation assessment consists of five chapters: Current Management Situation, Review of Technical Knowledge, Dynamics of Important Vegetation Communities, Conservation Status, and Information Needs. The Current Management Situation provides the history that led to the recognition that a particular owl species required special attention in research and management planning. The Review of Technical Knowledge chapter provides a summary of scientific knowledge on the target species. The review includes a critical assessment of the strength of scientific evidence upon which conclusions are based and therefore was written by recognized experts for each owl species. Be-

cause a majority of management activities influence these owls indirectly through changes in habitat conditions, each assessment includes a Vegetation Communities chapter. It provides an important link in understanding the relationship between the species' ecology and its conservation status. Forest dynamics set limits on management options for these owls and must be understood before management is formulated.

The Conservation Status chapter provides a synthesis of the scientific knowledge presented in the previous two chapters from the perspective of biological conservation. By conservation status, we mean the demographic condition of the species as it relates to the likelihood of local and national persistence of wild populations over the long term. Are populations of these owls in the United States currently threatened? Are current land management practices likely to imperil local or regional populations? This chapter is organized around critical questions concerning the biology of the owl. After answering these questions, which together define the status of the species, management considerations are discussed and the species' conservation status is summarized.

The final chapter, Information Needs, systematically examines the available knowledge to assess the need for new information before developing a conservation strategy for the species. The research identified through this process is then placed in the context of a research program.

We have approached the assessment process as a first step toward managing these species in the context of ecosystem management. Therefore we have organized the scientific knowledge reviewed in each assessment to answer particular questions necessary in formulating a conservation strategy. The degree to which these questions can be answered indicates the strength of scientific support for management decisions.

STANDARD FOR KNOWLEDGE

What is the basis for scientific knowledge? In producing the assessments, we reviewed refereed literature, nonrefereed publications, research reports, and data accumulated by resource management agencies. Not all publications on a species are referenced in the assessments, nor was all published material considered equally reliable. The topics reviewed were those judged most important in understanding the conservation status of a species and in formulating future management strategies. Because particular literature is not referenced does not

suggest that the work was judged inferior. Rather, the results may not have been directly relevant in a conservation framework or another paper may have demonstrated a similar result more directly.

The assessments emphasize refereed literature because this is the accepted standard in science. Nonrefereed publications or reports were regarded with greater skepticism. We chose to use some nonrefereed literature in the assessments, however, because of the paucity of peer reviewed research on forest owls in North America. Nonrefereed literature was particularly important in describing habitat use patterns across geographic regions. Data accumulated by resource management agencies, much of which are not contained in publications or written reports, were important in estimating the geographic distribution of the owls. These data required special attention because of the diversity of persons and methods used to collect the data. To maintain quality control, we followed up (by phone or mail interviews) on most cases where information from a single observation significantly extended the estimated distribution of a species.

LIMITATIONS

We emphasized research conducted in the United States and sought new distribution information largely for areas within the United States. Although we focus on owl populations within the United States, we recognize the influence of populations in Canada and south of the United States on the dynamics of owls in this country. Thus, we gathered broad distributional information on the species throughout North America and considered how variation in the biology of the species within, and outside, the United States might influence their status.

Boreal and great gray owls occur in circumboreal distributions so a majority of their ranges encompass lands in Europe and Asia. Research on these species in Europe and Asia is more extensive than in North America. We drew upon this literature in describing the general biology and ecology of the species, noting when information was derived from distant geographic areas. We expect that the ecology of these owls varies geographically, so we have been careful in drawing conclusions based largely on studies from Europe or Asia.

Because we sought to produce these assessments rapidly, we did not analyze existing unpublished data or attempt to conduct meta-analysis to synthesize information from published literature. Instead, the assessments are limited to literature summaries.

The timeline established for completing the assessments and resources available to write this report did not allow us to gather some critical information. In particular, we were unable to examine current federal land management plans to discern the direction of forest management and the potential impacts on the forest owls. We were also unable to gather sufficient information to assess trends in the abundance of old forest. Finally, although we recognize the utility of demographic analysis in assessing species' status, we were unable to build and examine demographic models for these owls based on existing demographic data.

DEFINITIONS

Several terms used throughout these assessments are defined below:

1. A "forest stand" is a homogeneous portion of forest that can be differentiated from surrounding units by variation in age, composition, structure, and/or geography (Daniel *et al.* 1979). For this report I suggest that a stand must be at least 0.25 ha.

2. "Microhabitat" refers to conditions within an area usually smaller than a forest stand—a site where an individual owl performs a single activity such as roosting, nesting, or foraging.

3. "Habitat use" refers to the occupation of a site by a species for some function. This term does not imply anything about the quality of the site to support the species.

4. "Habitat quality" refers to a continuous gradient in the ability of a site to support a species. High quality habitat provides conditions for a population to experience positive population growth.

5. "Suitable habitat" refers to conditions where the long-term balance between birth and death rates results in an expected finite rate of increase greater than 1. Conversely, unsuitable habitat refers to conditions where population growth over the long term results in λ less than 1 (see Chapter 2).

6. "Mature forest" refers to a forest stand that has developed long enough since catastrophic disturbance that mortality and regeneration are prominent processes and regeneration results from parent trees in the stand. The mature stand has tree-fall gaps created after stand establishment and an uneven tree diameter distribution (Hayward 1991).

7. "Old forest" or "old growth" refers to a forest stand in later stages of succession whose age and physical structure is currently influenced by processes within the stand rather than the last catastrophic disturbance. Old forest will have a wide variety of tree sizes and ages and a patchy structure resulting from tree mortality and regeneration (Hayward 1991).

In Chapter 2 we discuss the distinction among habitat requirements, preferred habitat, and selected habitat.

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Methods and Terminology Used With Studies of Habitat Associations

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The forest owl conservation assessments emphasize the relationship between flammulated, boreal, and great gray owls and the forests in which they occur. The habitat requirements of the owls and their principal prey bear strongly on the conservation status of the owls. Establishing the characteristics of the owl/habitat relationship is not a trivial or straightforward process. This discussion provides background on the study of habitat associations that will place the literature on owl habitat in theoretical perspective.

AN APPROACH TO ASSESSING HABITAT REQUIREMENTS

Habitat loss or degradation is a major threat to wildlife populations. Understanding the habitat requirements of a species is, therefore, critical to assessing its conservation status. Unfortunately, although the data gathered in most habitat studies may be useful, their actual analysis and interpretation are often flawed. Here I discuss habitat selection and methodology of habitat evaluation as a preamble to our analysis of existing information on the habitat of flammulated, boreal, and great gray owls.

In discussing habitat associations we must distinguish between habitat requirements, habitat preferences, and habitat use (occupancy). Habitat requirements are of greatest importance because they determine the fate of the population. They are, however, the most difficult habitat relations to resolve because they require estimation of a complex fitness function (figure 1). Habitat preferences, which may not be identical with requirements (Lack 1933), are best discerned through experimentation, although carefully designed statistical tests can reveal some aspects of preferences. Occupancy is simple to measure but can be misleading, particularly when occupancy is weighted by abundance of the target species. Each of these points is amplified below.

HABITAT REQUIREMENTS

Habitat requirements are revealed by the relationship between fitness and a habitat gradient (figure 1). Fitness, or some proxy for it, can in principle be measured along any such habitat gradient. The methods used to choose the gradient and to measure fitness are of great practical importance but do not influence the underlying logic discussed here. Various methods for measuring habitat use and availability, and their shortcomings, are discussed in detail by Morrison *et al.* (1992).

The habitat-specific fitness function can be uniform (identical fitness associated with all values along the habitat gradient) but is likely to be irregular in shape (e.g., figure 1). Fitness is influenced not only by the physical and structural features of the habitat gradient, but also by the biota that occupy some or all of it. This fact makes uniform fitness functions extremely unlikely in nature.

The points at which individuals can neither survive nor reproduce (figure 1) define the extremes of the "range of tolerance" of the species along that habitat gradient. A horizontal line, representing the fitness at which the population replaces itself but does not increase ($\lambda = 1$ or $r = 0$), cuts the fitness function at habitat values that define the boundaries between source and sink habitats. Sink habitat is defined as habitat in which individuals can survive and reproduce, but not at rates sufficient to maintain the population without immigration. The source-sink concept (Lidicker 1975) is familiar, but its relevance to conservation biology in general (Pulliam 1988), and to habitat evaluation in particular, has been overlooked.

A fitness function can be written for a single genotype or for an entire (genetically polymorphic) population. If the fitness function is for a single genotype, its maximum identifies the optimal habitat for that genotype, unless the replacement line is irregular (i.e., fitness required for replacement is not independent of habitat type), in which case the optimal habitat is indicated by the maximal positive difference between fitness and the replacement line.

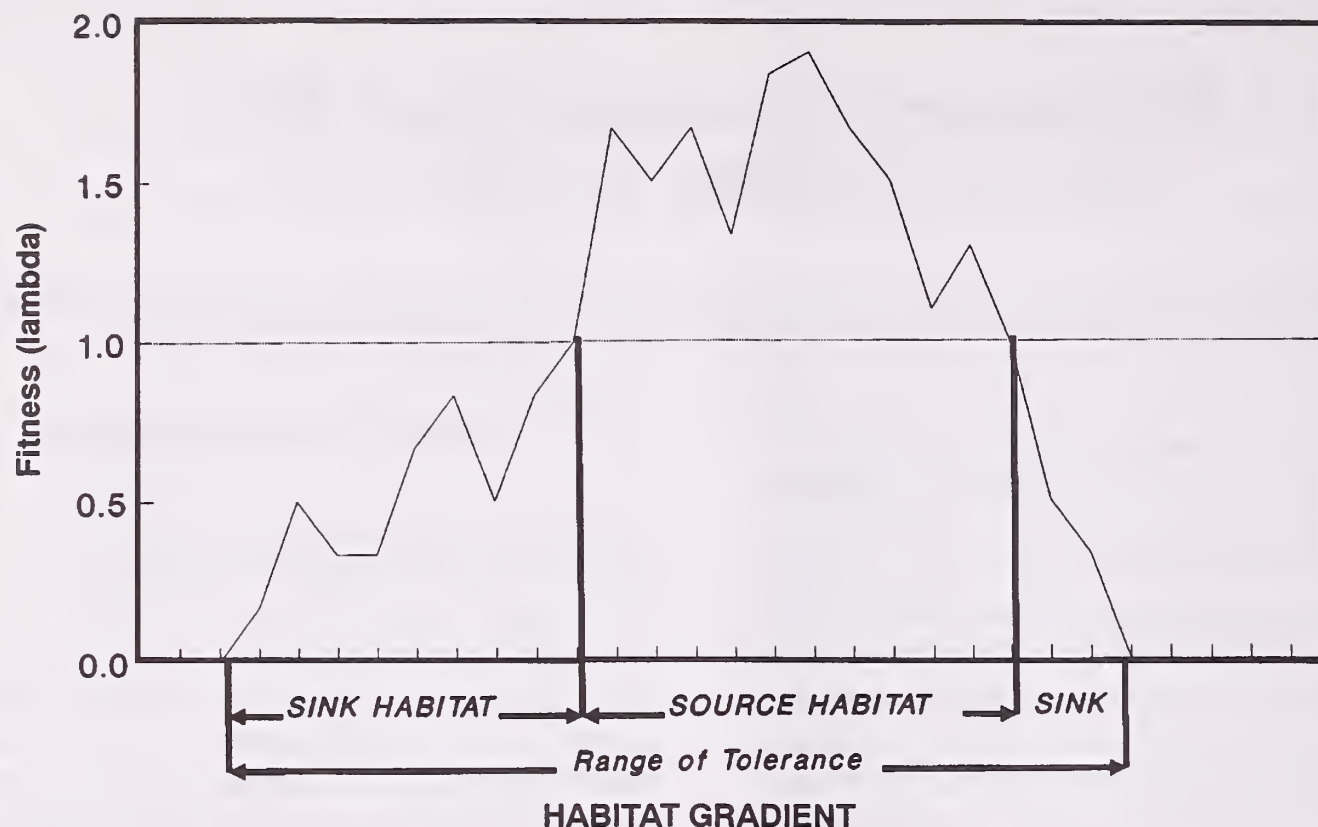


Figure 1.—Fitness (geometric rate of natural increase, λ) in relation to a habitat gradient. Growing populations ($\lambda > 1$) are sources of individuals for populations in habitat not capable of sustaining a stable population (sinks, $\lambda < 1$). All occupied habitats are within the range of tolerance.

If, however, the fitness function is a composite of the fitness functions of different genotypes, which is probably the case in most wildlife populations, it represents the weighted mean fitness of all genotypes occurring at each point on the habitat gradient. In this case, the maximum of the fitness function is controlled by the relative abundance of the various genotypes and indicates optimal habitat for the population, given the current mix of genotypes in the population.

Determination of fitness functions specific to genotypes requires genetic markers; determination of a composite fitness function requires only an adequate random sample of individuals occupying the gradient. Estimating the vital rates (e.g., fertility and mortality) required to write a fitness function can be extremely time-consuming, especially if they vary with age. Estimation of rates of survival from fledging to the age at which breeding begins is complicated by the difficulty of estimating rates of successful natal dispersal.

Habitat-specific fitness functions are critical to assessing habitat requirements because fitness is a direct measure of how well adapted a population is to a particular environment at a particular time. An accurate fitness function tells how well a population exploits different environments and thereby indicates which environments will best support the species in the long term. (It is nonetheless applicable

only to the population for which it was measured.) Measures such as population density, habitat use, and even habitat preference are proxies and are unneeded if fitness is truly known. If not interpreted carefully and cautiously, these proxies can be misleading.

HABITAT PREFERENCES

All treatments of habitat selection in birds assume selection is at least in part active; birds seek habitats on the basis of internalized standards (e.g., Lack 1933), rather than passively accepting random locations and then making the best of them. Active selectors necessarily have a preference function, i.e., a set of standards of desirability (preference) for different values of a habitat gradient. Accepting existence of a preference function in no way implies an assumption of consciousness on the part of the animal.

Such a preference function is potentially different from the fitness function along the same gradient because the genes (Jaenike and Holt 1991) and the learning that underlies the behavior necessary to find a site are not necessarily those underlying its optimal exploitation. The most preferred habitat can be sink habitat if evolution of the preference function lags behind evolution of the habitat-specific fitness function when the latter is changing rapidly, as when

natural selection is severe following a catastrophic change in the availability of habitat types or the invasion of a region by a superior competitor or predator (Van Horne 1983). One would expect natural selection to bring the two functions back into phase (Jaenike and Holt 1991). For the sake of simplicity, I will assume hereafter that the preference function accurately reflects the fitness function.

Aspects of preference can be identified by examining the relationship between occupancy and availability of habitat, but great care must be taken in interpreting such relationships because occupancy does not equal preference. Preferred habitat may not be available; occupied habitat and preferred habitat may therefore differ. It follows that occupancy patterns in some populations may actually obscure the true habitat requirements of the species because the individuals are merely doing the best they can under bad circumstances. Individuals will manifest preferences among available habitats as long as they have choice, even if all their options are suboptimal.

HABITAT SELECTION AND OCCUPANCY

Habitat selection is the process whereby preference is translated into occupancy. In classical habitat-selection theory (Fretwell and Lucas 1969, Fretwell 1972) and modern expansions of it (e.g., Pulliam and Caraco 1984, Pulliam 1988), individual animals assess habitat and settle where their potential fitness is highest. No one assumes that they actually calculate fitness. Rather, these models assume that internalized preferences, either innate or as templates subject to modification by learning (e.g., habitat imprinting), dictate the choice.

Habitat selection theory tends to focus on a single habitat dimension. But habitat preferences do not exist in a vacuum. Rather, they coexist with preferences on other habitat dimensions and at other spatial (e.g., nest-site and foraging range) and temporal (e.g., foraging and roosting) scales. Thus an individual may occupy suboptimal habitat on one dimension because of an absolute requirement on another dimension. An obvious example is that flammulated owls cannot nest in home ranges with high quality foraging habitat if no cavities exist there.

The habitat an individual actually occupies is influenced by the preference functions specific to its genotype, *and* by the availability of that habitat. Availability is a function of both the abundance of the habitat within the searching range of the would-be occupant *and* the number of individuals already occupying it. Interspecific competition and/or the danger of predation may also force individuals to

occupy suboptimal sites.

Because habitat occupancy is a function of *both preference and availability*, preference cannot be inferred from occupancy without also considering availability. According to the theory summarized above, densely occupied areas could be sink habitat (figure 1), which late-arriving or inferior competitors occupy temporarily while waiting for the opportunity to move into higher quality, preferred habitat. Sink habitat may be densely occupied because source habitat is producing a large surplus of individuals (e.g., Krebs 1971), which may mean that the population has an excellent probability of long-term persistence. Or, more ominously, sink habitat may be densely occupied because source habitat is rare but productive. In this case the sustainable population size is lower than the actual size and dependent upon the rare source habitat. If source habitat has recently been reduced in extent, a decline to a new and lower equilibrial population size can be expected, despite the current abundance of birds in the sinks. Obviously, abundance is not an infallible indication of habitat quality (Van Horne 1983, Vickery *et al.* 1992a,b).

It is possible, however, to make some valid inferences about habitat preference with a comparison of habitat occupancy and habitat availability (provided these can be measured accurately; see Morrison *et al.* 1992). The first step is to confirm that selection has taken place. A statistical test is used to test for differences between observed occupancy patterns and expected occupancy patterns under an assumption of random settlement. The expected pattern is given by the actual availability pattern. A significant difference indicates that settlement was nonrandom. Nonrandom settlement is habitat selection (active or passive). This statistical procedure tests the hypothesis that the species selects habitat along the gradient in question. It confirms that preference is manifested, but the statistical test itself does not identify the preference.

For example, it might be shown that the mean value of canopy coverage in occupied sites is significantly less than the mean value in all sites (or unoccupied sites). This shows that the birds have selected sites with respect to canopy coverage (or some factor correlated with it), and it suggests that they prefer relatively open sites (within the range of available structures), but it does not say that the mean canopy coverage of occupied sites is the value preferred by these birds. The most preferred condition may not even be available in the area sampled.

The second step is to inspect the data in an attempt to infer preferences. (This inference, of course, is

valid only for the population on which it is based. Extrapolation to other populations is not valid, because fitness and preference functions are context-specific.) The inference can be strengthened with information on the degree of habitat saturation. If the habitat is not saturated, occupied sites are likely to be the most highly preferred of those available. This inference is based on the assumption that each bird will occupy the site it prefers most, among the sites available to it (Alatalo *et al.* 1985). If the habitat is saturated (which itself is difficult to assess), then preferred habitat will not be revealed by comparing occupancy and availability. The extreme values of the occupancy pattern may well indicate the boundary between totally unsuitable and minimally acceptable sites (e.g., the dimensions of a nest cavity entrance would have such a minimum). Notice that "totally unsuitable" and "sink habitat" are not synonymous. In other words, saturated occupancy distributions may reveal the limits of tolerance of a species along a habitat gradient but can reveal little about optimal habitat.

This entire discussion has been focused on territorial species in which individuals can control territories and preserve the fitness differentials between them and lower quality habitat. In the limit, as intruder pressure reaches a level that makes territory defense uneconomical for the defender, territoriality will break down. At this point intruders should distribute themselves to maximize their individual expected fitness, with average fitness being equal across the habitat gradient once an equilibrium is reached. This special case, referred to as the ideal free distribution by Fretwell (Fretwell and Lucas 1969, Fretwell 1972), is a situation in which local density is an accurate indicator of habitat quality.

Interpretations of habitat occupancy patterns are hypotheses about the preferences of the species in question along the habitat gradient in question. Ideally such hypotheses should be tested experimentally to confirm that they have accurately identified the preferences of the population.

Keeping in mind the distinctions among fitness, preference, and occupancy should facilitate evaluation of published accounts of owl habitat use, most of which are anecdotal or qualitative assessments of habitat occupancy. In most cases occupancy patterns only suggest hypotheses about the habitat requirements of the species, but such hypotheses are useful in planning future research and current management.

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Part II: FLAMMULATED OWLS

Current Management Situation: Flammulated Owls

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The flammulated owl (*Otus flammeolus*) is a western mountain species associated mainly with ponderosa (*Pinus ponderosa*) and Jeffrey pine (*Pinus jeffreyi*) forests in the United States and Canada (see Chapter 4). As a neotropical migrant, this small forest owl occurs on national forests in the United States during the breeding season and winters mainly south of the border but also in southern Texas, Arizona, and California. Based on the owl's documented distribution (see National Geographic Society 1987, Johnsgard 1988), it may occur on 89 National Forests across 6 Regions. To establish the management status of flammulated owls throughout its range we queried management personnel on all National Forests where the species is likely to occur. Our questionnaire requested information on:

1. Documented breeding status of flammulated owls on the Forest (no records, recorded, recorded breeding).
2. The range of habitats in which this species has been recorded on the Forest.
3. The existence of any Forest or Regional level conservation strategies and/or management plans.
4. The management status of the species in each Region (state list, USDA Forest Service sensitive species list).
5. Whether forests are conducting distribution surveys for flammulated owls.
6. The distribution of flammulated owls plotted on a National Forest map based on all data available from the Forest data base.

The questionnaire asked for additional, more qualitative, information. For instance, we asked how forests are dealing with this species in biological evaluations (evaluating important habitat or population viability) and in monitoring plans. We were also interested in whether forests had information on changes in vegetation used by flammulated owls over the last two centuries.

We also reviewed refereed literature sources for documented owl sightings and locations where museum specimens were collected. Most of these

locations were plotted using U.S. Geological Survey 7.5" topographic maps. Where definite locations could be obtained they were plotted based on the latitude and longitude of the site. When locations were not clearly defined or described, the approximate center of the appropriate U. S. Geological Survey 7.5" topographic map was used. Forest Service source locations were plotted on 0.5 inch per mile Forest recreation maps using the same methods.

The distribution of flammulated owls based on literature and agency locations is depicted in Map 1. This map also displays the combined potential distribution of ponderosa pine and Jeffrey pine based on Kuchler's potential natural vegetation (Kuchler 1964). The owl locations and vegetation distribution were digitized and plotted on an existing map of the United States.

Flammulated owls were documented to occur on 72 of the 89 forests where the species may be expected. The owl has been recorded breeding on 24 of these forests. The flammulated owl is listed as a U. S. Forest Service "sensitive species" in four regions covering a majority of the owl's range (table 1). Despite this designation, specific Forest- or Regional-level management plans have not been written and in many cases presence/absence of the species has not been confirmed (table 2). General raptor management guidelines or general statements concerning nest protection refer to the flammulated owl on five national forests. The Payette National Forest in Idaho goes further than other forests by outlining a direction to develop management guidelines and indicating some interim management recommendations (Moore and Fredricks 1991). The direction on the Payette National Forest indicates (our synopsis):

1. Conduct nocturnal surveys of all forested areas within a project planning area for flammulated owls.
2. Develop 1:24,000 maps of all existing mature ponderosa pine, Douglas-fir, old ponderosa pine, and old Douglas-fir on the Payette and Hell's Canyon National Recreation area to

Table 1.—Status of the flammulated owl on National Forests as reported by managers in early 1993.

Region	No. of Forests in Region	No. of Forests where owl is present	No. of strategies or plans in place	Addressed in Forest management plan?	Forest Service conservation status
Northern	13	13	None	No	Sensitive
Rocky Mountain	12	10	None	No	Sensitive
Southwestern	11	11	None	No	Sensitive
Intermountain	16	13	1	No	Sensitive
Pacific Southwest	18	14	None	1 Forest	None
Pacific Northwest	19	10	None	4 Forests	None
Eastern		Not reported in this Region			
Alaska		Not reported in this Region			

determine the extent of available habitat.

3. Develop permanent monitoring areas in managed and unmanaged areas to determine population trends.
4. Implement uneven-aged management in flammulated owl habitat.
5. Develop plans to retain mature to old ponderosa pine.
6. Retain areas of high flammulated owl densities until population viability, habitat requirements, and effects of forest fragmentation on flammulated owls are known.
7. Provide snags for meeting the nesting requirements of flammulated owls. Live trees must be preserved in harvest areas to provide for future snag recruitment.
8. Encourage and support studies of the relationship of flammulated owl habitat requirements to forest management practices.

The Northern and Intermountain Regions reported that forests within their region are conducting flammulated owl surveys on a regular basis. All other Regions and the southern portion of the Intermountain Region were recording and documenting flammulated owl locations, but only incidental to Northern spotted owl (*Strix occidentalis caurina*), California spotted owl (*Strix occidentalis occidentalis*), and Mexican spotted owl (*Strix occidentalis lucida*) surveys.

In addition to its designation as a sensitive species by the USDA Forest Service, flammulated owls are given special management status in four states: Idaho (Species of Concern), Montana (Species of Concern), Oregon (Sensitive), and Washington (Candidate). Arizona, California, Colorado, Nevada, New Mexico, Texas, Utah, and Wyoming have not given the owl any special status.

The response we received from National Forests throughout the range of flammulated owls indicates that little is known about the species in these management units. Furthermore, there is no mechanism in place to gather data necessary for management on most Forests. On Forests where some attempt has been made to manage flammulated owls or raptors in general, there appears to be little scientific basis for those management recommendations.

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Table 2.—Habitat associations of flammulated owls based on surveys of USDA Forest Service data bases. Habitat is described by dominant overstory tree species: PP - Ponderosa pine forest, DF - Douglas-fir forest, MC - Mixed conifer forest, QA - Quaking aspen forest, SF - Spruce-fir forest, LP - Lodgepole pine forest, WF - White fir forest, JP - Jeffrey pine forest, CP - Coulter pine forest. Status for National Forests who did not respond is listed as "not present."

State	Forest	Occurrence	Habitats
Northern Region (Region 1)			
Montana	Beaverhead	Suspected	
Montana	Bitterroot	Present	Low Elev. DF, PP
Idaho	Idaho Panhandle	Present	Mature, PP, DF
Idaho	Clearwater	Present	DF, PP
Montana	Custer	Suspected	
Montana	Deerlodge	Present	Low Elev. DF, PP
Montana	Flathead	Present	Low Elev. DF, PP
Montana	Gallatin	Suspected	
Montana	Helena	Suspected	PP, DF
Montana	Kootenai	Present	PP, DF
Montana	Lewis and Clark	Suspected	Low Elev. PP, DF
Montana	Lolo	Present	Mature, PP, DF
Idaho	Nez Perce	Present	PP
Rocky Mountain Region (Region 2)			
Wyoming	Bighorn	Suspected	
South Dakota	Black Hills	Not present	
Colorado	Grand Mesa	Present	PP, Oak, MC
Wyoming	Medicine Bow	Suspected	
Colorado	Rio Grande	Present	SF, MC, PP
Colorado	Arapahoe/Roosevelt	Present	PP/DF
Colorado	Routt	Suspected	
Colorado	Pike/San Isabel	Breeding	PP
Colorado	San Juan	Breeding	PP
Wyoming	Shoshone	Suspected	
Colorado	White River	Present	
Nebraska	Nebraska	Not present	
Southwest Region (Region 3)			
Arizona	Apache/Sitgreaves	Breeding	PP, PP/QA, MC
New Mexico	Carson	Breeding	PP, PP/QA, MC
New Mexico	Cibola	Breeding	PP, PP/QA, MC
Arizona	Coconino	Breeding	PP, PP/QA, MC
Arizona	Coronado	Breeding	PP, PP/QA, MC
New Mexico	Gila	Breeding	PP, PP/QA, MC
Arizona	Kaibab	Breeding	PP, PP/QA, MC
New Mexico	Lincoln	Breeding	PP, PP/QA, MC
Arizona	Prescott	Breeding	PP, PP/QA, MC
New Mexico	Santa Fe	Breeding	PP, PP/QA, MC
Arizona	Tonto	Breeding	PP, PP/QA, MC
Intermountain Region (Region 4)			
Utah	Ashley	Suspected	LP, PP, DF
Idaho	Boise	Suspected	
Wyoming	Bridger-Teton	Not present	
Idaho	Caribou	Breeding	Mature DF
Idaho	Challis	Suspected	PP

Table 2 - (continued),

Utah	Dixie	Not present	
Utah	Fishlake	Present	MC, SF
Nevada	Humboldt	Suspected	PP, MC
Utah	Manti-La-Sal	Breeding	PP
Idaho	Payette	Breeding	PP, DF
Idaho	Salmon	Breeding	PP, DF, SF
Idaho	Sawtooth	Suspected	LP, SF
Idaho	Targhee	Suspected	LP, DF, MC
Nevada	Toiyabe	Suspected	JP, WF
Utah	Uinta	Suspected	
Utah	Wasatch-Cache	Not present	

**Pacific Southwest Region
(Region 5)**

California	Angeles	Breeding	JP, CP
California	Cleveland	Breeding	JP, CP, DF
California	Eldorado	Present	
California	Inyo	Present	
California	Klamath	Present	DF, MC, PP
California	Lassen	Present	PP/JP, MC
California	Los Padres	Present	JP
California	Mendicino	Present	MC
California	Modoc	Present	JP, MC
California	Six Rivers	Present	WF, DF, PP
California	Plumas	Present	MC
California	San Bernardino	Present	PP, JP
California	Sequoia	Present	PP, MC
California	Shasta-Trinity	Present	MC, DF
California	Sierra	Not present	
California	Stanislaus	Not present	
California	Tahoe	Not present	
California	Lake Tahoe	Not present	

**Pacific Northwest Region
(Region 6)**

Oregon	Deschutes	Breeding	MC, PP
Oregon	Fremont	Not present	
Washington	Gifford Pinchot	Present	WF, PP, LP, MC
Oregon	Malheur	Breeding	WF, PP, LP, MC
Washington	Mt. Baker	Not present	
Oregon	Mt. Hood	Not present	
Oregon	Ochoco	Not present	
Washington	Okanogan	Breeding	
Washington	Olympic	Not Present	
Oregon	Rogue River	Not present	
Oregon	Siskiyou	Not present	
Oregon	Siuslaw	Not present	
Oregon	Umatilla	Breeding	
Oregon	Umpqua	Present	WF, PP, LP, MC
Oregon	Wallowa-Whitman	Breeding	
Washington	Wenatchee	Present	WF, PP, LP, MC
Oregon	Willamette	Present	
Oregon	Winema	Present	WF, PP, LP, MC
Washington	Colville	Not present	

Review of Technical Knowledge: Flammulated Owls

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INTRODUCTION

The flammulated owl (*Otus flammeolus*) is a tiny, common predator on invertebrates that nests in cavities in western North American coniferous forests. It was thought by early workers to be rare (Bendire 1892, Bent 1938), but more recent opinion is that it is common but secretive (Marshall 1967, Winter 1971, 1974, Richmond *et al.* 1980). The combination of its very small size (Earhart and Johnson 1970), ventriloquial but low-pitched voice (Miller 1947), strictly invertebrate diet (Ross 1969, but see below), and probable migratory behavior (Winter 1974, Balda *et al.* 1975, but see Johnson 1963) suggests an unusual adaptive strategy. Understanding all aspects of this strategy will lead to wise management decisions.

The flammulated owl is the next-to-smallest North American owl (15-17 cm long, 45-63 g mass in non-breeding season) and among the smallest of its large and cosmopolitan genus. Females are slightly larger than males, but there are no sexual, age, or seasonal differences in adult plumage. Body plumage is gray with black shaft streaks and crossbars and varying degrees of rufescent wash. Flight feathers and wing coverts are gray to brown with lighter bands. Reddish birds are rare in North America.

Dark eyes distinguish it from all other owls of similar size in its North American range. Additionally, size and short ear tufts distinguish it from other American *Otus*. In the field, it is much more often heard than seen. Low-pitched, faint, hoarse, and ventriloquial mono- or disyllabic hoots throughout the breeding season rule out all other forest owls except the long-eared owl (*Asio otus*). If seen, the flammulated owl is easily identified by the unique combination of small size and dark eyes.

Despite its seeming abundance, the flammulated owl does not have a high reproductive rate. As it apparently is restricted to forests of commercially valuable tree species, timber management practices may influence its viability. Baseline population data are sparse and insufficient to model its population dynamics. In addition, virtually nothing is known about its range, habitat, or diet in winter.

Knowledge of the flammulated owl is based on a broad but rather shallow literature. Most publications are anecdotal. Four population studies, begun since 1980, form the foundation of our knowledge. By far the most important of these was begun at Manitou Experimental Forest, west of Colorado Springs, Colorado, in 1981 (Linkhart and Reynolds 1987; Reynolds and Linkhart 1987a,b, 1990a,b, 1992). This study, which has continued through the present, has documented all aspects of the population biology of the species, including movements (Linkhart and Reynolds 1987; Reynolds and Linkhart 1987a, 1990a), breeding biology and food habits (Reynolds and Linkhart 1987b), home range use (Linkhart 1984), pair relations (Reynolds and Linkhart 1990a), longevity (Reynolds and Linkhart 1990b), habitat use (Reynolds and Linkhart 1992), and study techniques (Reynolds and Linkhart 1984, Reynolds 1987).

The only other study that has exceeded 2 years was conducted in the Zuni Mountains of western New Mexico from 1981-1986. The emphasis of this study was breeding biology and habitat use (McCallum and Gehlbach 1988, McCallum *et al.* in review). It was the only one of the major studies not to employ radio-tracking. Radio-tracking studies that focused on habitat use but that also produced some information on breeding biology were conducted in the Blue Mountains of northeastern Oregon from 1983 to 1984 (Goggans 1986) and on Mt. Wheeler near Kamloops, British Columbia, from 1989-1991 (van Woudenberg 1992). The Oregon study was conducted in the Starkey Experimental Forest, site of two shorter-term studies (Bull and Anderson 1978, Bull *et al.* 1990).

SYSTEMATICS

Phylogenetic Position

The genus *Otus* is unanimously classified in the Strigidae (typical owls), which, along with the Tytonidae (barn owls), constitute the order Strigiformes. Most authorities consider another

group of night birds, the Caprimulgiformes (nightjars and allies), to be the sister taxon of the Strigiformes. (The taxonomic history of these groups is summarized by Sibley and Ahlquist 1990:402-411.) Sibley and Ahlquist's (1990) classification, based on DNA-DNA hybridization, supports the conventional linkage of these two orders. Cracraft's (1981) resurrection of the 19th-century idea that owls and the Falconiformes are closely related has not been widely accepted. Most authorities apparently prefer convergent evolution as an explanation for the similarities in the raptorial lifestyles of "hawks" and owls.

The position of *Otus* within the Strigidae is of interest because of the possibility that *O. flammeolus* is a primitive member of its large and well-defined genus. Sibley and Ahlquist (1990:figure 362), using DNA-DNA hybridization, united *Otus*, *Asio* (including long-eared (*A. otus*) and short-eared (*A. flammeus*) owls), and a large group including *Bubo* and *Strix* in an unresolved trichotomy. Randi *et al.* (1991), using allozymes, consistently found *Otus* to be more closely related to *Bubo* than to *Asio*. The earliest fossil of *Otus* is from the Miocene (Johnsgard 1988).

Species Status

The most recent treatment of *Otus* (Marshall and King 1988) places more emphasis on vocalizations than morphology and none on molecules. Although the emphasis on vocalizations is plausible (Marshall 1967), some vocal similarities, like similarities in plumage, could be the result of convergent evolution. The systematics of the genus *Otus* has not been subjected to biochemically based analysis.

The position of *O. flammeolus* within *Otus* has been the subject of much debate in the systematic literature. The species was first mentioned in 1854 by Lichtenstein (Ridgway 1914) and described in more detail in 1859 by J. J. Kaup, from two specimens obtained in Mexico. It remained rare in collections for decades, but its specific identity was not challenged until Delacour (1941) merged it with the widespread Old World *Otus scops* complex. He based this decision on the sharing of finely patterned plumage, presumed migratory behavior of northern populations, and voice (Voous 1989). This decision has not met with widespread acceptance and might be considered a symptom of the Holarctic overlumping that gripped avian taxonomy at mid-century. Other authors (Marshall 1966, 1967, 1978; van der Weyden 1975, Hekstra 1982) have agreed that *Otus flammeolus* is more closely related to the Old World scops owl subgenus than to the New World screech-owl sub-

genus. In particular, it is vocally allied to all but one Old World species, which have high-pitched slow songs (< 3 notes per sec) that contain 1-4 notes. Like them, it has no secondary song, and females do not duet with their mates. The other New World species, all of which are considered screech owls, have lower-pitched rapid songs (>3 notes per sec) that contain > 4 (often considerably more) notes; they do have secondary songs and females duet (van der Weyden 1975).

The position of *O. flammeolus* in the subgenus *Otus* (scops owls) has recently been revised. According to Marshall and King (1988), the closest relative of the flammulated owl is the pallid scops owl (*O. brucei*), a migratory species that breeds from the Middle East to Pakistan. They base this position on the similarly low and unaccented hoots of *O. brucei* (Roberts and King 1986). The *Otus scops* superspecies (*O. scops*, *O. senegalensis*, and *O. sunia*) is more similar morphologically than *O. brucei* to *O. flammeolus*, but "the normal song of *Otus scops* is a high-pitched staccato whose chirping quality runs identically through the differently timed songs of its far-flung races.... It is inconceivable that a female of *scops* would recognize the singing male *flammeolus* as a potential mate and vice versa. They cannot be in the same species" (Marshall 1966:240).

The male hoots of the flammulated owl are the second lowest in frequency of 37, mostly larger-bodied, species of *Otus* examined by van der Weyden (1975). Indeed, this note is barely higher than the equivalent vocalization of the much larger long-eared owl (McCallum, pers. obs.). Miller (1947) explained that an unusually large tracheal diameter and thick, loosely attached vibratile membranes make it possible for this small owl to produce such a low frequency sound.

The voice and the structure responsible for it obviously constitute an autapomorphy. The possible function of this distinctive and often-discussed derived character has not been ascertained. The flammulated owl throughout its range lives near one or more species of *Bubo*, *Strix*, and *Asio*, all effective nocturnal predators. Voous (1989:53) "is tempted to suppose that, in order to survive, the flammulated owl simulates greater size and strength by its bravado and ventriloquial voice, at the same time behaving elusively and inconspicuously by night and day." The mechanism by which such vocal mimicry might benefit a prey species has not, however, been proposed.

Subspecies and Geographic Variation

Of the two "Mexican" specimens examined by Kaup in 1859, one type was grayish, the other rufous (Phillips 1942). It was understandable at the time to assume that they represented the usual gray and red phases found in other species of *Otus*, rather than representing regional variation. For the next 80 years museum workers assumed the flammulated owl was a permanent resident throughout its range, presumably by extension from other (mostly larger) owl species. Phillips (1942) corrected this impression by showing that verified dates of occurrence north of Mexico fell between April 11 and October 31. He also surmised that the type was a migrant from the northern part of the range, rather than a resident of southern Mexico, where most of the birds are more rufous in color. With the breeding range of the type unknown, the name *O. f. flammeolus* could not be applied to a known population, which in the opinion of one authority, "precludes the objective use of subspecific names" (Voous 1989:54).

Nevertheless, up to six subspecies have been described, often on the basis of limited samples. *O. f. rarus* Griscom was based on two large reddish birds from Guatemala (Phillips 1942), while *O. f. idahoensis* (Merriam) was based on a short-winged bird from the northern United States. Breeding of the species has not been demonstrated in Guatemala, so *rarus* is thought to be a migrant, perhaps from southern Mexico (Phillips 1942), perhaps from the interior Pacific Northwest, which caused Marshall (1978:9) to consider it synonymous with *idahoensis*. But Hekstra (1982) retained both *rarus* and *idahoensis* and described another Guatemalan subspecies, *meridionalis*, said to be "smaller and glossier than *rarus*" (Hekstra 1982:56), as well as another northern subspecies, *borealis*, said to be duller than *rarus* and *idahoensis*. Finally, Hekstra (1982) described *frontalis* from the Front Range of Colorado as browner than *flammeolus*, with very black shaft streaks. These subspecies were not based on new data but on reinterpretation of old specimens.

Differences in coloration of the kind used by Hekstra to erect subspecies are said by Marshall (1967) to vary in parallel among sympatric species of *Otus* and thus have no taxonomic value. He therefore recognizes no subspecies of *O. flammeolus*. Marshall (1967) speculated that the color and patterning in an area match tree trunks and foliage found there. For example, the redder birds found in Middle America were said to blend with red-barked trees found there. Moreover, variation due to differ-

ential fading, dependent upon local climate and the amount of exposure to sunlight on day roosts, plus postmortem fading of skins, has produced taxonomic confusion in all *Otus* (Marshall 1967:5). And, individual plumage variation is continuous rather than dimorphic in the flammulated owl, hence greater than in other *Otus*, which are thought to have two distinct color phases, with "red" caused by a dominant autosomal allele (Marshall 1967:1). The source of Marshall's statement, however, is not given. Hrubant (1955) showed that for the eastern screech-owl three phenotypic phases could be explained by a single-locus, 3-allele model with graded dominance. The apparently continuous phenotypic variation in *O. flammeolus* suggests polygenic control of plumage variation or at least a multi-allele, incomplete dominance hypothesis such as Hrubant's. Neither hypothesized mode of gene action has been the subject of formal genetic analysis for the flammulated owl.

On the basis of 32 fall (i.e., fresh-plumaged) birds thought to be on their breeding grounds, Marshall described a smooth cline of increasing wing-length and mass from southeast to northwest, presumably correlated with the length of the migratory route (Marshall 1967:24). Great Basin-Rocky Mountain birds are blackest, with broadest shaft streaks and least red trimming. Patterning becomes finer and redness increases to the northwest (the extreme for fineness is in the Pacific Northwest) and southeast (the extreme for redness is on the Mexican Plateau, Marshall 1967:24).

Fossil History

Modern *Otus flammeolus* remains have been recovered from the Pleistocene San Josecito Cave, Aramberri, Nuevo León (with *O. asio* (*sensu lato*) and *O. trichopsis*); from the late Pleistocene Samwel Cave, Shasta County, California (no other *Otus*) (Wetmore 1956). The earliest fossil of *Otus* is from the Miocene (Johnsgard 1988)(see Voous 1989).

DISTRIBUTION AND ABUNDANCE

Recognized Distribution

The flammulated owl is known to occur from southern British Columbia south and eastward to Guatemala and probably El Salvador. Its western limit is the western limit of open pine forests between the latitudinal extremes, and it ranges no closer to the Atlantic than the Rocky Mountain escarpment and the Sierra Madre Oriental. Except during the

migratory period, it is with very rare exception found only in montane forests, usually open conifer forests containing pines. Its breeding range in North America is well delineated. The non-breeding range of these northern birds is not known. The year-round range in Middle America is sketchily described and open to question.

In conjunction with surveys for other owl species, and in some instances surveys targeted for flammulated owls, the USDA Forest Service has accumulated records for flammulated owls in the western United States. These data are summarized in Chapter 3 and Map 1. They confirm the widespread occurrence of the species in previously documented parts of its U. S. range, particularly California, Arizona, New Mexico, and southern Colorado. These data also show that it is widespread in west central Idaho, just east of the previously known stronghold in the Blue Mountains of Oregon. It was found in a few new locations in Utah and Montana but remains virtually undocumented on the east slope of the Cascades in Oregon and Washington, where it probably occurs. The species remains undocumented from lodgepole pine (*Pinus contorta*) forests of Wyoming, as well as from ponderosa pine forests in eastern Montana, Wyoming, and the Black Hills.

Breeding Range

North America.—Nesting has been confirmed or adults observed during the breeding season in southernmost British Columbia (Okanagan and S. Thompson Valleys, Fraser River north to Riske Creek, Rocky Mountain Trench, [Howie and Ritcey 1987, R. J. Cannings pers. comm.]), the east slope of the Cascades, and interior ranges of Washington, Oregon (e.g., Blue Mtns., Goggans 1986, Bull *et al.* 1990), northeastern California (Johnson and Russell 1962), and western Nevada. It has been found in most forested ranges of Nevada, including some lacking ponderosa pine (Herron *et al.* 1985, S. Garland, pers. comm.), but the range is poorly documented in Utah. In California (Winter 1974) it is found in summer throughout the Cascades, Sierra Nevada, forested parts of the coast ranges from Del Norte County south to Monterey County, the Transverse ranges, and the Peninsular ranges. Previous to this study (Chapter 3) it was poorly known in the northern Rocky Mountains states (Holt *et al.* 1987). There remain no records from the Black Hills, where seemingly suitable habitat occurs. The species is widespread in Colorado (Webb 1982), New Mexico (Hubbard 1978), and Arizona (Reynolds and Linkhart in press). It breeds in the Guadalupe, Davis,

and Chisos Mountains of Texas (Oberholser 1974).

Middle America.—The few available records support the presumption that it breeds primarily in the Sierra Madre Occidental, Sierra Madre Oriental, Sierra Madre del Sur, and the Volcanic ranges of central Mexico. Breeding south of Mexico has not been confirmed. This owl is known in northwestern Mexico from the Sierra Madre Occidental (Sonora and Chihuahua [Stager 1954, Marshall 1957] and Sinaloa [Hubbard and Crossin 1974]). In the northeast it occurs near the Big Bend of the Rio Grande in the Sierra del Carmen (Miller 1955), in an isolated range in central Coahuila (van Hoose 1955), in the Sierra Madre Oriental of eastern Coahuila (van Hoose 1955, Ely 1962) and western Nuevo León (Hubbard and Crossin 1974), and on isolated Cerro Potosí (S. N. G. Howell pers. comm.). In central and southern Mexico breeding is thought to occur in the state of Mexico (AOU 1983), Las Vigas, Veracruz (Sutton and Burleigh 1940), and probably on Cerro San Felipe in Oaxaca, where one was heard in April (Binford 1989) and a specimen was found in June (J. C. Arvin *vide* S. N. G. Howell). Early statements that it breeds south to Guatemala were based on the assumption of residency of winter specimens (Phillips 1942).

Nonbreeding Range

In North America, it occurs in lowlands peripheral to breeding habitat in October, sparingly in November, and occasionally in December. Three midwinter specimens (from Arizona, Louisiana, and California) are the only dependable winter records. An unpreserved specimen and two sight records in Montana (Holt *et al.* 1987) are poorly documented and dubious. An aural record in New Mexico in March (Collins *et al.* 1986) by D. A. McCallum was probably a long-eared owl (based on subsequent observations and spectrographic analysis, DAM). The same is perhaps true for a January aural record in lowland riparian habitat in Arizona (Monson and Phillips 1981) and perhaps some March records (see the Migration section below).

The midwinter range in Middle America is very poorly understood. The species has not been observed in the northern tier of Mexican states during this period. There are a few specimens and aural records in breeding habitat localities farther south (Sinaloa [3-4 Dec., Hubbard and Crossin 1974], Jalisco [22 Feb., Schaldach 1969], Michoacán [Friedmann *et al.* 1950], Guerrero [Navarro 1992], Distrito Federal [Friedmann *et al.* 1950, 20 Dec., Wilson and Ceballos in press], Guatemala [AOU 1983],

and El Salvador [22 Dec., Marshall 1978:9, specimen lost]). If, as suggested above, the flammulated owl breeds in Oaxaca, then these winter localities may also be breeding localities. On the other hand, Navarro (1992) found the species during winter but not during the breeding season in the Sierra de Atoyac of Guerrero. Two large, long-winged birds taken in Guatemala (see *O. f. rarus* above) are thought by Marshall (1978:9) to have been migrants from the population breeding in the Pacific Northwest.

Estimates of Local Abundance and Population Trends

Flammulated owls were considered rare until the 1960's, and quantitative baseline data on abundance are not available. Many field guides and compendia now refer to this owl as "locally common." Most authorities (e.g., Marshall 1967, Richmond *et al.* 1980, Marcot and Hill 1980) believe that because of its "secretive" habits the flammulated owl simply went undetected in much of its range until ornithologists and birders, following Marshall (1939, 1967), began imitating calls to incite vocal responses by territorial males. This procedure enabled collectors to begin an assessment of the U. S. and Middle American range in the 1950's and 1960's (Marshall 1967) but contributed little to understanding of densities [although up to 10 birds were sometimes called into one location (e.g., Johnson and Russell 1962)]. Subsequently birders contributed materially to filling in details of the distribution (e.g., Winter 1974, Collins *et al.* 1986), but less attention was paid to numbers. In the 1980's, the four population studies in Colorado, New Mexico, Oregon, and British Columbia began to produce local density estimates (see the Local Density Estimates section). Numerous surveys, many incidental to surveys for the spotted owl (*Strix occidentalis*), have been conducted in recent years (Chapter 3). These recent data suggest that flammulated owls are among the most abundant birds of prey in some areas.

Recent surveys, plus old collecting localities, can be used as a baseline for assessing subpopulation persistence on the basis of presence/absence data. Marshall (1988) revisited the site of his earlier study (1939) and found flammulated owls absent from the portion of the study area that had been logged. Marshall also failed to find the species at Sutton and Burleigh's (1940) site in Veracruz. These observations, plus Franzreb and Ohmart's (1978) finding that the owls were present in mixed conifer forest but absent from nearby logged sites, suggest that elimination and replacement of yellow pine (e.g., ponde-

rosa or Jeffrey pine) and mixed conifer forests by Europeans have reduced the overall abundance of the flammulated owl.

Although suitable habitat probably has declined somewhat, human-caused habitat modification (vs. outright elimination) in the past century (e.g., selective logging, fire-suppression) may have caused undetected increases or decreases in numbers of flammulated owls. Which, if either, has occurred is a matter of speculation, as no historic data exist for drawing a firm conclusion. (See Response to Forest Change section for a discussion of these issues.)

Recent developments in molecular biology, however, make it possible to assess population changes within the twentieth century indirectly by comparing past and present population genetic structure. Small populations lose genetic variation as a result of genetic drift. Current populations, therefore, should be genetically less variable than those at the turn of the previous century if a population bottleneck occurred during the interim. Amplification of microsatellite DNA with the polymerase chain reaction (PCR) is now a fairly routine procedure, and it has been applied successfully to museum skins of birds (D. B. McDonald, pers. comm.). Although few nineteenth century skins of flammulated owls exist in museum collections, there are sufficiently large series from the early part of the present century (McCallum pers. obs.) to allow such a comparison to be made.

MOVEMENTS

Migration

The flammulated owl, at least its North American populations, is now considered a neotropical migrant (e.g., Winter 1974, American Ornithologists' Union 1983, Johnsgard 1988, Voous 1989). This conclusion is based on plausibility rather than hard data, as no banded flammulated owl has ever been recovered outside the immediate vicinity of its original capture site.

The species was originally assumed nonmigratory, presumably by extension from other owls, most of which are permanent residents (Phillips 1942). The assumption was plausible because this insectivore was also assumed to be facultatively carnivorous like other *Otus*, which it is not (Ross 1969, but see Food Habits). Phillips (1942) compiled the earliest and latest dates of verified occurrence for each U. S. state and Canadian province and concluded that flammulated owls breeding north of Mexico are trans-latitudinal migrants. Johnson (1963), while

agreeing that the owls are absent from North American breeding grounds during winter, noted the lack of low elevation records (i.e., transients) in Middle America and hypothesized altitudinal migration supplemented with facultative torpor in northern populations. Numerous submontane records in North America are consistent with either long distance or altitudinal migration.

Winter (1974) reviewed the evidence for and against torpor and altitudinal migration and concluded that the species is a trans-latitudinal migrant. There is only a handful of documented lowland records in midwinter in the United States (Collins *et al.* 1986). The flammulated owl appears incapable of entering torpor (Banks 1964, Ligon 1968, J. D. Ligon in Winter 1974, Webb 1982), as do other small owls (Ligon 1969). When experimentally subjected to low temperatures without access to food, they maintain normal body temperatures with high metabolic rates and lose up to 25% of body mass. Moreover, vagrants found in Florida, Alabama, Louisiana, Texas, and on an oil rig in the Gulf of Mexico (Collins *et al.* 1986) reveal the ability of individual flammulated owls to cover long distances. Vagrancy of this magnitude is not often associated with sedentary species (Winter 1974). Finally, the low level of geographic variation in plumage, compared to that of the sedentary screech owls, suggests that gene flow is high (Winter 1974).

Three winter records in Montana, although second-hand and undocumented with specimens or photographs, have been published (Holt *et al.* 1987). There is also an unsubstantiated Christmas Bird Count record from Washington. While each of these records is individually unlikely, collectively their geographic concentration carries some weight. Facultative carnivory would allow the flammulated owl to spend the northern winter on or near the breeding grounds, but experience with captive birds suggests that successful carnivory on adult vertebrates is extremely unlikely. A recent observation by Cannings (pers. comm.) suggests that flammulated owls may take prey from leaf litter, which might allow overwinter survival in some areas (see Food Habits).

The Middle American distribution of the species is so incompletely understood that it is impossible to state with any confidence the migratory status of populations breeding in Mexico. Most winter records are south of 20° N. Lat., so northern Mexican populations may be migratory. Those breeding in southern Mexico are more likely to be resident because winter records are in breeding habitat. Age and sex differences in migration and other movements are

unknown.

Nomadic behavior is unlikely to be found in this species. Very high site fidelity has been recorded in the best-studied population in Colorado (Reynolds and Linkhart 1987a, 1992). Also, the flammulated owl preys on insects and other invertebrates and appears to take whichever of several alternate prey taxa are most abundant at the time and location (Goggans 1986, Reynolds and Linkhart 1987b). Neither characteristic is typical of nomadic species, such as the snowy owl (*Nyctaea scandiaca*, Parmelee 1992) and boreal owl (*Aegolius funereus*, Hayward and Hayward 1993). On the other hand, recent population fluctuations of flammulated owls in the Kamloops and Okanagan areas of British Columbia have been interpreted as a numerical response to spruce budworm outbreaks (St. John 1991, A. van Woudenberg, pers. comm.).

Timing and Routes of Migration

Flammulated owls evidently remain in their breeding areas well into October (e.g., October 12, Linkhart and Reynolds 1987), when they become vocal after completing their annual molt (Marshall 1967). North American birds apparently migrate southward primarily in October, peaking in northern Arizona when large noctuid moths are most abundant (Balda *et al.* 1975).

Autumn records in the lowlands are from October and November. Several November records along the U. S. Gulf Coast, one in central Texas, and repeated records (mist-netted) in the southeastern plains of New Mexico (mostly in spring) suggest that a portion of the population may migrate east of the breeding range, perhaps wintering in the Sierra Madre Oriental (where so far the species has not been recorded in winter) or even the U.S. Gulf Coast.

The earliest lowland aural record (Bill Williams River, Arizona, 9 March-18 April 1979, Monson and Phillips (1981)) could be of a migrant, an overwinterer, or misidentified. Some March singers identified as flammulated owls may be long-eared owls, but a sight record near Boulder, Colorado 5-28 March 1966 suggests earlier arrival in breeding habitat is possible. They return north below breeding habitat, primarily in April (Balda *et al.* 1975). Spring arrivals (first dates for singing birds) are mostly in late April-early May in North America (see Phenology of Courtship and Breeding). Some females arrive on breeding grounds as early as males, but others appear later (Reynolds and Linkhart 1987b).

HABITAT OCCUPANCY

Concepts summarized earlier in this book, under Methods and Terminology Used With Studies of Habitat Associations, make it possible to evaluate the information content of published accounts of the habitat of the flammulated owl, most of which are anecdotal or qualitative assessments of habitat occupancy. I have synthesized the observed occupancy patterns into the following composite hypothesis about the habitat requirements of the flammulated owl. A detailed summary of the information used in formulating this hypothesis follows.

Composite Requirements

The common features of reported flammulated owl habitat are a cold temperate and semiarid climate, high abundance or diversity of nocturnal arthropod (mostly insect) prey, open physiognomy, and some dense foliage (used for roosting). Nesting habitat also includes cavities or nest boxes. Occupied forest types (ponderosa pine and Douglas-fir) have the highest insect diversities in the climatic zone occupied by the species (Reynolds and Linkhart 1987b). Open physiognomy seems a requirement in light of the use of thinned Douglas-fir forest in drier parts of British Columbia (Howie and Ritcey 1987). Semiaridity may be a correlate of open forests or it may be a physiological requirement of the species. Warmer microclimates are occupied within the generally temperate elevations occupied by these birds (Reynolds and Linkhart 1987b), but they are uncommon in lower elevation woodlands, perhaps because of structural deficiencies there. Prey availability appears responsible for the migratory behavior of this species, in light of the fact that small carnivorous owls do not migrate, while small insectivorous owls apparently do, but only from locations with seasonal subfreezing temperatures. Cavities are clearly required unless acceptable nest boxes are provided.

A Hierarchical Scheme for Summarizing Information on Habitat

Several authors (e.g., Hildén 1965, Johnson 1980, Hutto 1985) view habitat selection as hierarchically organized with more specific levels nested within more general ones. This seems particularly apt for migratory birds. Brewer and Harrison (1975) suggest, however, that most birds probably choose habitat and even home range before leaving on their first fall migration. Migrants may use hierarchical ordering for navigating to a location they chose previously,

but choices of large-scale factors such as range and forest-type may simply involve staying in their natal habitat. In cases where individuals disperse prior to fall migration, hierarchical choice may occur directly.

Reynolds and Linkhart (1990a) have shown that adult owls examine other territories during the breeding season and that territory occupancy in the subsequent year may be influenced by these forays. This phenomenon and territory fidelity (Reynolds and Linkhart 1987a) remind us that adults base current-year site selection on knowledge obtained in the previous year(s). Nothing is known about the timing of habitat selection by juveniles, for they disperse in late summer, and only one has been recaptured in subsequent years (Reynolds and Linkhart 1990b).

Nonetheless, the hierarchical approach is useful for organizing data on habitat use. Moreover, the hierarchical levels are good first approximations of independent axes for the fitness and preference functions of the birds. What is inferred from the habitat requirements of flammulated owls will be described at the following scales for breeding, fall migration, winter, and spring migration.

1. Geographic range
 - history
 - climate
 - elevation
2. Landscape
 - vegetation type
 - home range vegetation
3. Home range/territory
 - foraging habitat
 - roosting habitat
4. Microhabitat
 - singing sites
 - foraging sites
 - nest sites and cavities

Geographic Range

The geographic range of the flammulated owl, when compared to the ranges of other species, reveals significant aspects of its physiological, behavioral, and ecological tolerances.

Biogeography of Related Species

The genus *Otus* occupies temperate and tropical latitudes of all continents but Australia and Antarctica. At the least, then, the potential range of *O. flammeolus* is that of its genus. This species, however, is restricted to the temperate zone and part of the tropics of one continent, North America. Moreover, except for migration, it is further restricted to mon-

tane elevations with seasonally temperate climates. Tropical lowlands appear inhospitable.

Like most species whose migration does not carry them across the equator, the flammulated owl does not have disjunct populations in the South Temperate Zone of the Western Hemisphere. It is more common for birds to have populations in the North Temperate Zones of both North America and Eurasia, but this phenomenon is restricted to boreal species whose ranges extend into Beringia (e.g., black-billed magpie (*Pica pica*) and northern hawk owl (*Surnia ulula*)). No species of *Otus* is boreal in distribution.

Otus scops has been considered the ecological equivalent of *O. flammeolus* in Eurasia. The two species have been suggested to be sister taxa, with vicariant historical biogeography, which would explain the absence of *O. flammeolus* from the Old World. But as it turns out (see below), the flammulated owl is a montane pine forest specialist, which is not the case with the scops owl. Ecologically, if not phylogenetically, the scops owl is more similar to the low-elevation generalists *O. asio* and *O. kennicottii* than to the flammulated owl (Voous 1989).

Distinctive Features of the Owl's Range

When compared to unoccupied areas in North America, the range of the flammulated owl is very revealing. First, it is strictly western, like the ranges of many species, but unlike most of these does not extend to the Pacific coast. (Based on available data, National Geographic Society (1987) and Johnsgard (1988) are erroneous in this regard.) Second, it is strictly montane, but unlike the ranges of many western montane species it does not extend farther north than southern British Columbia. Finally, it extends south to Guatemala and El Salvador, but only in interior mountain ranges. The only other species range with a similar pattern is that of the pygmy nuthatch (*Sitta pygmaea*), which is identical in British Columbia and in Mexico, and differs mainly in including coastal pine forests of central California. The combined ranges of the western population of the Nashville warbler (*Vermivora ruficapilla*), the Virginia's warbler (*V. virginiae*), and the Colima warbler (*V. crisallis*), which constitute a superspecies (AOU 1983), are very similar to that of the flammulated owl.

The range of the flammulated owl is essentially coextensive with that of mid-elevation montane pine forests. Pines (see below) may be important or even necessary, but they are not sufficient to guarantee the presence of the flammulated owl. The pygmy nuthatch is thought of as a yellow pine specialist, but it has a sister taxon in lowland southeastern pine

forests, where the flammulated owl is absent, and it occurs abundantly in coastal pines of the central California fog belt. These two areas differ from the range of the flammulated owl in being humid and/or hot. If the flammulated owl summers from British Columbia south to southern Mexico and winters from southern Mexico to El Salvador, migrating southward in the uplands mainly in October and northward in the lowlands mainly in April, as is now believed, then the species occurs year-round in a semiarid cool temperate climate and nowhere else. It leaves the northern part of its range during winter, when the adult lepidopterans, coleopterans, and orthopterans it eats are unavailable. The exceptions to this pattern are the few fall and winter records from the southern United States.

Climate and Thermoregulation

The thermoregulatory abilities of the flammulated owl have not been studied (except for attempts to induce torpor), but some tentative inferences may be drawn from studies of its congeners. Specimens of *Otus trichopsis* and *O. kennicottii* from Arizona were very effective at regulating body temperature when subjected to high ambient temperatures, as long as humidity was low (Ligon 1969). A similar thermoregulatory strategy may be the reason *Otus flammeolus* is absent from humid areas.

On the other hand, the screech owls Ligon (1969) studied, especially the smaller *Otus trichopsis*, had rather high lower critical temperatures. This might suggest a heavy energetic cost of thermoregulation for the even smaller flammulated owl in low ambient temperatures. Whatever the cost, flammulated owls meet it. Males do not use cavities for day-roosting or resting at night during the early nesting season, when temperatures often fall below -6° C (R. T. Reynolds, pers. comm.). The fact that spring snowstorms lead to mass loss and death (Ligon 1968, Webb 1982) suggests that food availability is the key to thermoregulation. Starving owls lose up to 25% of their body mass before dying (Winter 1974).

It should be remembered, moreover, that Ligon's measurements were necessarily taken on inactive birds. For nocturnal owls, the period of greatest activity is also the period of coldest temperatures. Heat produced by foraging activity at night may be used to maintain body temperature. Male flammulated owls are very active while provisioning their mates early in the breeding season. The females spend most of this time in their nest cavities. Possibly neither experiences serious cold stress, as long as noctuid moths (the main food at this season, Reynolds and Linkhart 1987b) are plentiful.

Elevational Range

The flammulated owl occurs mostly in mid-level conifer forests that have a significant yellow pine (i.e., *Pinus*, subgenus *Pinus*, section *Pinus*, subsection *Ponderosa* (Critchfield and Little 1966)) component. In addition to floristic differences, higher elevation forests are generally cooler and more humid; lower elevation woodlands are hotter and more arid. The elevational specificity of the owl may stem from thermoregulatory limitations and hence results from climatic factors. On the other hand, the elevational limits of the species may be determined by the availability of prey species, which in turn is determined ultimately by the tree species present and proximally by temperature (R. T. Reynolds pers. comm.). Climate therefore may influence the distribution of the species indirectly through the prey base rather than directly through its thermoregulatory abilities. Finally, the flammulated owl may be physiologically and ecologically capable of occupying a much broader range of the elevational gradient than is occupied but be competitively excluded from the portions of the gradient it does not occupy. Limitation through avian competitors seems unlikely, as the pool of potential avian competitors changes considerably over the latitudinal range of the species. Mammalian nest-site competitors (sciurids) and food competitors (bats) are more plausible causes of competitive limitation (see Community Ecology).

The migratory routes of this species remain essentially unknown. Balda *et al.* (1975) captured 20 birds during spring in pinyon-juniper woodland (elevation 2040 m) in New Mexico, but none during spring in ponderosa pine forest in Arizona (elevation 2510 m). Just the reverse occurred in fall, 25 being captured or observed in the ponderosa site in Arizona, while none were captured in the lower site in New Mexico. These results suggest that breeding habitat, or habitat just below it, is used during north-south movements, but a series of sight records published in *American Birds* (McCallum unpubl.) shows that even lower elevations are used in both spring and fall.

Landscape (Vegetation Type)

Both floristics (the purely taxonomic component of habitat) and structure are merged in the concept of vegetation type, so this category and the next (structure of home range habitat) overlap. I will limit this section to discussions of gross vegetation types and summarize quantitative studies of habitat structure in the following section. This discussion is limited to breeding habitat, as only anecdotal informa-

tion exists for habitat used outside the breeding season.

General Floristics

Reynolds and Linkhart (1992) reported that all published North American records of nesting, save one, came from forests in which western yellow pine (essentially *Pinus ponderosa* and *P. jeffreyi*) was at least present, if not dominant. There are several other forest types that also contain cavities suitable for nesting by this species, including low elevation riparian zones, pinyon-juniper woodland, Douglas-fir forest, and spruce-fir forest. Because these are virtually unoccupied, while yellow pine forest types are densely occupied, preference for yellow pine is suggested. Exceptions include several occupied mountain ranges in Nevada that lack yellow pines but support breeding owls in old aspen stands (S. Garland pers. comm.). One nesting record from the Argus Mountains of California was in an old pinyon forest (Huey 1932), and the species occurs in pinyon-juniper stands containing no ponderosa pine on the Colorado plateau (R. T. Reynolds, pers. comm.). McCallum and Gehlbach's (1988) study site was an old pinyon woodland, but all home ranges did contain some ponderosa pines. The range of the species extends far to the south of the ranges of *P. ponderosa* and *P. jeffreyi*, but numerous other species of subsection *Ponderosae* are present in the highlands of southern Mexico and southeastward (Critchfield and Little 1966). As all of these pine occur at mid-elevations on rather xeric mountain slopes, the influence of floristics and various correlates of the elevational range at which these species occur cannot be disentangled (see above).

Howie and Ritcey (1987) noted the flammulated owl's strong association with the very dry submontane interior Douglas-fir zone and absence from the ponderosa pine zone. These Douglas-fir forests, however, had been selectively logged in the past and approximated the structure of ponderosa pine forests to the south (see next two sections).

Characteristics of Entire Home Range

In Colorado, male foraging, territorial defense, resting, and day-roosting were restricted to home ranges averaging 14.1 ha during the pre fledging period (minimum polygon method, range = 8.5-24.0, sd = 5.0; Jennrich-Turner [1969] model: mean = 20.0, range = 13.5-34.0, sd = 7.0). Range size appeared determined by canopy volume and range shape by topography (Linkhart 1984). Ranges of females are not known but were probably much smaller, as females were fed by males during incubation and the early nestling period.

Reynolds and Linkhart (1992) compared percentage representation of four vegetation types in the territories (103 ha) and in the entire study area (452 ha). A chi-square test of their data (Reynolds and Linkhart 1992) was highly significant (chi-square = 22.672, $df = 3$, $P < 0.001$). Inspection of cell chi-squares suggest that old ponderosa pine/Douglas-fir is favored and young Douglas-fir/blue spruce (a more closed, colder, and humid forest type) is disfavored. Preference for old forest was further supported by observations of foraging owls. Trees in which arthropods were captured had a mean age of 199 years, compared to 111 years for a random sample from the study area (Reynolds and Linkhart 1992).

Additional support for the hypothesized preference for old forest comes from the frequency of occupation of individual territories during the 12-year study. Those territories that were in continuous old ponderosa pine/Douglas-fir forest were occupied with few interruptions by a succession of males. Those with < 75% of this forest type were occupied only as long as the original male returned (1-3 years). Moreover, during the 12-year study only one male changed territories from one year to the next, and he moved to a traditional territory with a much greater complement of old-growth forest (Reynolds and Linkhart 1990a).

In Oregon five home ranges mapped via radio-tracking averaged 10.3 ha (minimum convex polygon method, range = 5.5-19.3, $sd = 6.3$) (Goggans 1986). Goggans speculated that they were smaller than home ranges in Colorado because the broken canopy in Oregon allowed more grass and shrubs to grow, which may in turn harbor more arthropods than the closed-canopy forest in Colorado. It should be noted, however, that three of her five home range estimates included no data for the incubation period, when home ranges are largest (see below), while Linkhart's (1984) estimate of 14.1 ha included no data from the postfledging period, when home ranges are smallest. The Oregon and Colorado data, then, are not comparable.

Marcot and Hill (1980) analyzed the vegetation composition of seven so-called territories in northwestern California and found that California black oak (*Quercus kelloggii*) was as ubiquitous (67%) as yellow pine (50% presence). These "territories," however, were actually singing sites. Both Goggans (1986) and Reynolds and Linkhart (1987a,b) have documented singing by unmated territorial males. The habitat Marcot and Hill (1980) described is therefore not necessarily suitable for nesting. Moreover, some of these birds were called in with tape record-

ings, and hence may not have been singing from within their defended areas.

Oak (*Quercus* spp.) has been mentioned in numerous accounts, particularly those of Marshall (1957) and Marcot and Hill (1980). Marcot and Hill (1980) noted that the California black oak provides many cavities, which may be important for nesting. They did not compare occupied habitat to that available, but they did note that occupied areas had certain characteristics generally associated with the species. These include association with ridge tops and xeric mid-slopes, two-layered canopies, tree density of 1270 trees/ha, and basal area of 58 m²/ha.

In British Columbia, "most owls were found in mature-old growth stands of Douglas-fir that had been selectively harvested 20-30 years prior to our surveys" (Howie and Ritcey 1987:251). Occupied habitat on Wheeler Mountain, which had the highest densities of flammulated owls, featured canopy closure of only 35-65% and many old Douglas-firs and ponderosa pines, with thickets of regenerating Douglas-firs. This site is especially instructive, because it implies that the structure, rather than the floristics, of a site is most important to these owls. In common with sites farther south, Wheeler Mountain habitat was mature to old forest, the canopy was multi-layered and open, and the area was punctuated with thickets. No owls were found in clearcuts or stands < 80 years old. Another factor possibly related to occupancy of these sites was a spruce budworm outbreak. After the budworms defoliated the small Douglas-firs they crashed, and the owls disappeared (A. van Woudenberg, pers. comm.).

Goggans (1986) remarked that home ranges were on upper slopes and plateaus, where ponderosa pines and Douglas-firs grew, and did not overlap dense mixed conifers in draws. Confinement of owl territories to south slopes, ridgetops, and plateaus is a characteristic of a variety of other sites as well (e.g., Marcot and Hill 1980, Reynolds and Linkhart 1987a, McCallum and Gehlbach 1988, Bull and Anderson 1978). These aspects experience more solar radiation and hence more evapotranspiration than more shaded microhabitats. The resulting deficit in soil moisture affects both the floristics (favoring drought tolerant species) and structure (leading to wide spacing among plants) of the vegetation.

Home Range

Foraging Areas

The flammulated owl's preference for yellow pine and/or Douglas-fir has been linked to prey availability. Reynolds and Linkhart (1992:168) noted that

"there are up to four times as many lepidopteran species associated with Douglas-fir and ponderosa pine than other common western conifers" (Furniss and Carolin 1977). High prey diversity and the structure of these forests may both favor successful foraging by flammulated owls. Foraging, then, may be one reason yellow pine forest types seem favored over higher elevation spruce-fir and lower elevation pinyon-juniper.

In Colorado, foraging (80% of radio-telemetry locations) was concentrated in 1-4 intensive foraging areas (IFAs) averaging 1 ha per range. One of these usually overlapped the nest (Linkhart 1984). The IFA nearest the nest was used during peak feeding times at dawn and dusk. More distant IFAs were used late at night when nest visits were less frequent. "Twelve of 15 (80%) IFAs were associated with mature, mostly open patches of ponderosa pine mixed with Douglas-fir on mid-slopes and ridgetops, and had exposures between 90-270 degrees" (Linkhart 1984). A multiple comparison of use and availability of forest types within territories showed significant selection of patches of old ponderosa pine/Douglas-fir and avoidance of patches of both young conifer and mature aspen vegetation (Reynolds and Linkhart 1992).

Goggans (1986) found that flammulated owls foraged more than expected by chance in stands with low to medium stem density. They also favored ponderosa pine and Douglas-fir over mixed conifers and grassland. But forest/grassland edge was most preferred of all, when compared to all forests and grassland.

These studies of actual use of home ranges for foraging are supplemented by studies of the structure of habitat immediately surrounding the nest, where foraging is concentrated during the nestling period (Linkhart 1984). The most quantitative study is that of McCallum and Gehlbach (1988). They evaluated vegetation structure around 17 independently chosen nest cavities. Some cavities were used more than once during the 6-year study, but a use was not considered independent if either bird had used the cavity before. Vegetation around occupied sites was compared to the vegetation around a matched set of the nearest available cavities (of appropriate size) that were not occupied. The study was designed to reveal nest-site selection, not territory selection.

Nest-site characteristics are summarized in table 1. Both a variance and a means test showed the owls in New Mexico were selective with respect to vegetation. Principal components analysis and stepwise discriminant function analysis were used in post hoc analyses to hypothesize the criteria of choice. The first principal component was interpreted as a suc-

cessional gradient, and occupied sites had significantly lower variance on this gradient than did unoccupied sites. This result indicates high selectivity on the successional gradient. The discriminant analysis showed that the mean values of occupied and unoccupied sites differed on this gradient. The two results lead to the hypothesis that flammulated owls prefer open, mature vegetation around the nest. A further post hoc analysis, suggested by the data, showed that shrub densities were lower in front of cavity entrances than they were behind them. In only 2 of 17 cases did an owl choose a site less desirable than the nearest alternative, according to the discriminant function. In one of these, both the used and unused sites were comparatively undesirable, and neither site was used again. The other case involved a nest that was 10 m from its previous alternative site in a year following much human disturbance in front of the previous year's nest.

McCallum and Gehlbach (1988) felt that the owls may have chosen sites with low shrub cover in front of the nest in order to have a clear flight path to the nest. They observed that owls approaching and leaving some nests did so within 2 m of the ground, below the cavity. In fact, it may be that they fly low because of the open vegetation, rather than preferring sites that allow them to fly low. Reynolds and Linkhart (1987b) have shown that flammulated owls forage intensively near the nest, and that open vegetation is preferred for foraging. This could explain the apparent preference of the New Mexico owls for open vegetation as well.

Bull *et al.* (1990) assessed both habitat structure and nest-tree characteristics on the Starkey Experimental Forest in the Blue Mountains of northeastern Oregon. (Starkey was also the site of Goggans's (1986) population study.) Availability was assessed by measuring a subset of these variables around unoccupied but minimally suitable cavity trees. Means of continuous variables they measured are summarized in table 1. Univariate tests comparing used and available sites suggested nonrandom occupancy. The analysis covered 10 variables, each with $\alpha = 0.05$, which lowers confidence in the inferences reached about habitat selection. Apparently, selection is indicated at some lower level of confidence. Ridges, upper slopes, south slopes, and east slopes apparently were selected, as in Colorado (Linkhart 1984) and perhaps in British Columbia (Howie and Ritcey 1987, slope position only). Stands with trees > 50 cm dbh (diameter at breast height) appeared to be preferred, and although 58% of nests were in ponderosa pine/Douglas-fir forest types, this percentage did not differ from availability.

Table 1.—Habitat characteristics of nest-sites of flammulated owls in two regions. The two Oregon studies were both in the Starkey Experimental Forest. Cavity entrance and cavity floor are maximal linear measures of each. Species diversity was calculated as $H' = \sum (p_i)(\log_2 p_i)$ where p_i = proportion of individuals in species "i". Species importance values (IVs) were relative density + relative basal area + relative frequency. Pinyon IV - ponderosa IV was calculated because pinyons outnumbered ponderosas in the general vegetation, but more nests were in ponderosas. Sample sizes are in parentheses.

Feature	New Mexico McCallum and Gehlbach 1988	Oregon Goggans 1986	Oregon Bull <i>et al.</i> 1990 (n = 33)
Cavity/nest tree			
Tree height (m)		26.6±12.0 (20)	24 ± 9.1
Tree dbh (cm)	46.2±10.7 (17)	56.3±11.9 (20)	72 ± 14.4
Cavity height (m)	4.89±1.60 (17)	10.0 ±5.9 (20)	12 ± 4.7
Cavity depth (cm)	21.2±5.2 (15)	20.4 ± 15.9 (9)	
Cavity entrance (cm)	5.9±0.9 (16)	7.2±1.4 (9)	
Cavity floor (cm)	13.5±2.8 (15)	16.5±1.5 (9)	
Surrounding woody vegetation			
Tree density /ha	504±416 (17)	589±451 (20)	330±146
Shrub density /ha	442±619 (17)		480±296
Basal area (m ² /ha)	2.1±1.26 (17) ¹	23.7±19.4 (20)	
Distance to opening (m)		< 30 (20)	50±51.3
Pinyon IV - ponderosa IV	102±196 (17)		
Canopy height (m)	10.1±1.80 (17)		
Canopy closure (%)			55±20.1
Number of canopy layers		> 1 (20)	2.5±0.5
Slope gradient (%)		16-25 (20)	18±11.8
Plant species diversity (H')	1.45±.337 (17)		

¹ Recalculated from original data.

Roost Sites

In contrast to foraging habitat, preferred roosting habitat appears to be dense vegetation. Goggans (1986) located 35 roost sites and found that none was in pure ponderosa pine forest, although the owls roosted disproportionately in mixed-conifer forest with a ponderosa pine component. Multilayered stands were favored, and mean stem density and basal area in 0.008-ha plots around roost trees were 2016 trees/ha and 129 m²/ha (vs. 589 trees/ha and 23.7 m²/ha for territories, cf. table 1). Although these Oregon owls avoided pure stands of ponderosa pine for roosting, they strongly selected ponderosa pines for roost trees within mixed-conifer stands. Colorado owls did not roost preferentially in ponderosa pine but usually used large Douglas-firs or ponderosa pines with sprawling form, which may have the dense foliage found in thickets elsewhere. Mistletree may augment the usefulness of such trees for roosting (R. T. Reynolds, pers. comm.). Thickets of regeneration are said to be used for roosting in British Columbia (Howie and Ritcey 1987) and are available on all territories studied in New Mexico (McCallum and Gehlbach 1988).

Linkhart (1984) found that mean distances from roost sites to the nest decreased from < 100 m to < 20 m just before fledging. In Oregon, mean distances

from roosts to the nest were 24.9 m (n = 5) during the nestling stage, but greater before and after (Goggans 1986).

Microhabitat

Roost Sites

In second-growth forests, roosting flammulated owls typically perch at the base of a horizontal limb, next to the trunk. Their generally gray plumage, highlighted with rufous, blends well with the bark of younger, "blackjack" stage, ponderosa pines, which is generally gray, the reddish color of more mature bark appearing between the plates. This same effect occurs on younger, higher limbs of old ponderosa pines. The remarkable crypsis of owl plumage against pine bark may be responsible for the nonrandom use of ponderosa pine as roosting sites in Oregon (Goggans 1986).

Singing Sites

Marshall (1939) noted that singing sites were well up in tall trees. Reynolds and Linkhart (1992) used radio-tracking to locate the exact tree singing birds occupied in 22 cases. Only ponderosa pines and Douglas-firs were used, and these averaged 289 years of age, compared to 111 for the random sample

of trees. Owls "sang from hidden positions next to tree trunks or in dense clumps of foliage" (Reynolds and Linkhart 1992:167).

Foraging Sites and Maneuvers

In Colorado, three of four foraging tactics (hawk-gleaning, hover-gleaning, and hawking) occurred in the more open lower two-thirds of tree crowns, either within the crown of a single tree or in the space between two trees (Reynolds and Linkhart in press). In late summer both adults and fledglings drop-pounced to the ground, grasses, or shrubs (Reynolds and Linkhart 1987b). In northeastern Oregon the most commonly taken prey were Orthopterans, most of which were probably taken from the ground, grass, and shrubs (Goggans 1986). All of these foraging sites are more likely to occur in open mature forests than in dense even-aged stands of young trees. Indeed, trees in which arthropods were captured had a mean age of 199 years, compared to 111 years for a random sample from the study area (Reynolds and Linkhart 1992).

The wings of flammulated owls are relatively long (Earhart and Johnson 1970), perhaps a constraint of migratory behavior. Long wings increase speed, but at the cost of higher wing-loading, which reduces maneuverability (R. Å. Norberg 1987). Limited maneuverability may contribute to preference for hunting in open forest and the near absence of flammulated owls from dense forest types. Indeed, Reynolds and Linkhart (in press) remark that foraging flights of flammulated owls are surprisingly high in speed. Bats, many of which are moth specialists, are known for very slow speed and great maneuverability. And hovering, a common foraging maneuver (Reynolds and Linkhart 1987b), is more efficient with slow wing-beat frequency, which requires low wing-loading and/or low aspect ratio (U. M. Norberg 1979). Perhaps flammulated owls hover inefficiently. Another correlate of low wing-loading and slow flight, low aerodynamic noise, is apparently superfluous for an insect-eater. Low wing-loading also reduces power demands when carrying prey but may not be important for this species because prey mass is low (prey are always single-loaded, Reynolds and Linkhart 1987b). It is at least possible, therefore, that the restriction of this owl to open forests is forced upon it by aerodynamic constraints resulting from its (presumed) migratory behavior.

Characteristics of Nest Trees and Nest Cavities

Because flammulated owls are secondary cavity-nesters, the presence of suitable cavities is an abso-

lute prerequisite of successful nesting. It does not follow, however, that all defended territories necessarily contain suitable cavities. It is known that not all territorial males have mates (Goggans 1986, Reynolds and Linkhart 1987a). Less experienced or subordinate males may defend territories with no adequate nesting sites rather than emigrating. It may fall to females to decide the adequacy of territories for nesting. This logical possibility is mentioned to underscore the danger of assuming that male presence is an indicator of habitat sufficiency. Successful nesting is the only criterion of habitat sufficiency.

Moreover, as almost all cavities used for nesting have been excavated by woodpeckers, site quality is constrained by the species of woodpeckers present and the tree species they have to work with. In the northernmost part of its range the flammulated owl uses cavities excavated by the pileated woodpecker (*Dryocopus pileatus*). In one Oregon sample the occupancy rate of pileated woodpecker cavities was significantly higher than the availability rate (Bull *et al.* 1990). Goggans (1986) found no difference between availability and occupancy of pileated woodpecker cavities in the same area of Oregon. The southern part of the range overlaps the former range of the now (nearly?) extinct imperial woodpecker (*Campephilus imperialis*), and their cavities may have been favored in the past as well. The central part of the range, however, has neither of these large woodpeckers, and northern flicker (*Colaptes auratus*) cavities, which are underutilized in Oregon (Bull *et al.* 1990), and sapsucker (*Sphyrapicus* spp.) cavities appear to be the main cavity resource (see Complex Interactions).

Characteristics of nest-trees and nest-cavities are straightforward to assess once nests are found, and several such studies have been done. McCallum and Gehlbach (1988) measured a suite of characteristics (table 1) and used multivariate statistics to test the hypothesis that flammulated owls were selecting cavities nonrandomly from the source pool of minimally acceptable cavities. Means tests were not significant, but variance tests showed nonrandom occupancy had occurred. Evidently the owls had a strong preference for the cavity values that happened to be modal in the pool of woodpecker cavities. It should be emphasized that this analysis addressed nest-site selection within territories, not selection of the territories themselves.

Goggans (1986) measured similar variables and likewise found no differences among the means of occupied and minimally acceptable but unoccupied cavities. She did not employ a variance test. Except for cavity depth, her results (table 1) appear no more

variable than McCallum and Gehlbach's (1988), and it appears that the owls used a narrow range of available sites in her Oregon study area as well as in their New Mexico area. Bull *et al.* (1990), working in the same area, found no difference between used and available cavity sites with regard to tree species, or dbh, but nest-trees were significantly taller than unused trees.

Scale Effects

Because seemingly basic requirements are disparate, habitat selection necessarily occurs on several potentially independent dimensions. Sites acceptable for some functions may not be occupied because requirements for other functions are not found nearby. McCallum and Gehlbach (1988) reasoned that flammulated owls in their New Mexico study area were more limited by foraging habitat around the nest than by nest-cavity characteristics *per se*. They based their conclusion on the finding that the owls selected cavities that were modal in the source pool while preferring vegetation that was rather extreme (i.e., in the tail of the source-pool distribution).

A certain amount of irony attends nest-site selection in this species. Males clearly select territories without female influence, as shown by the existence of unmated but territorial males in both Colorado (Reynolds and Linkhart 1987a) and Oregon (Goggans 1986). Males "show" nest-sites to females, which then choose the nest cavity from those offered by the male (Reynolds and Linkhart 1987a). Because males tend to roost and forage close to the nest-tree (Linkhart 1984, Goggans 1986), their mates essentially choose for them the areas in which they will carry out these important and time-consuming activities. Reynolds (*pers. comm.*) suspects that females choose mates on the basis of provisioning rates. If this is the case, then females sample habitat quality indirectly through the foraging efficiency of the males.

Seasonal Difference in Habitat

Although it is highly likely that the flammulated owl is a trans-latitudinal migrant (Winter 1974), all data supporting this conclusion are circumstantial. If northern birds do not leave their breeding latitude, they must either hibernate, prey on vertebrates, or, in the southern United States, migrate downslope to habitats in which arthropods are available in winter. Each of these options, discussed in detail under Migration above, would involve habitat or prey

shifts. Hibernation is unknown for strigiformes, and caves are not present in much of the flammulated owl's range. Flammulated owls appear unable to process the bones of mature vertebrates in captivity (M. Altenbach *pers. comm.*, Johnson and Russell 1962), so this option remains unlikely. Downslope migration seems plausible (Johnson 1963), but this would flood lowland riparian areas with birds, a phenomenon that would seem to be readily apparent in this restricted and well-studied habitat.

FOOD HABITS

Feeding

Food Capture and Consumption

The flammulated owl eats mainly nocturnal arthropods and hunts exclusively at night. A hunting bird locates prey from a perch visually, then flies to capture it aerially, to glean from needles (while hovering) or branches, or to pick it up from the ground. Marshall (1939) described hawkers as returning to the same perch while Reynolds and Linkhart (1987b) described hawkers as landing on a new perch. Captive fledglings used their feet to capture prey, including moths taken in an upside-down position from a ceiling. These captives swallowed soft-bodied prey whole, but large grasshoppers were held in the feet and torn apart with the bill (Richmond *et al.* 1980).

Foraging has been observed only during the nesting season. The distribution of feeding visits to the nest (Hayward 1986, Reynolds and Linkhart 1987b, McCallum *et al.* in review) suggests peak activity about 1 hour after sunset and 1 hour before sunrise, but this pattern has not been tested for non-nesting birds.

Most foraging in Arizona was aerial or in foliage (Marshall 1957). In Colorado, hawk-gleaning and hover-gleaning from needles were the most frequently used foraging tactics through the time of fledging (Linkhart 1984, Reynolds and Linkhart 1987b). In late summer both adults and fledglings drop-pounced to the ground, grasses, or shrubs (Reynolds and Linkhart 1987b). In northeastern Oregon, Orthopterans, the most available and most commonly taken prey (table 2), were 2.2 times more abundant in contiguous grassland than in pine forest where nests were located (Goggans 1986).

Acuity of the senses has not been investigated, but hearing may not be as important as for carnivorous owls, in that flight is not silent and the combs on the leading edges of the wings are not well developed. Karalus and Eckert (1974) reported a direct attack

by an owl sitting a quarter mile away after the squeak of a mouse was simulated, but their description suggests another owl species was under observation.

Diet

Major Food Items

The flammulated owl preys almost exclusively on invertebrates. No vertebrates were delivered in > 200 hr of observation at 37 nests (>2000 prey items observed) by Reynolds (pers. comm.). Similarly, McCallum *et al.* (in review) observed no deliveries of vertebrates in 141 hr of observation at four nests.

Several authors have reported stomach contents of breeding owls (table 2), Ross's (1969) study of 46 stomachs being the largest and most extensive geographically. Reynolds and Linkhart (1987b) sampled flying insects with a black-light trap from 20 May through 18 September (1981 and 1982) in central Colorado. They identified food items by observing males provisioning females and nestlings. Goggans (1986) sampled available arthropods from May through August 1984 in northeastern Oregon with 6 ground-level and 6 aerial (2.1 m above ground) window traps. She used remote photography to identify 311 prey items brought to nestlings (6 July-14 August, 1983 and 1984) but did not evaluate diet

before or after this stage. Anecdotal reports of invertebrate food do not enlarge the taxonomic list given in table 2.

In North America during summer, Orthoptera, Lepidoptera or Coleoptera predominate in the diet, depending upon availability (table 2). "Noctuids appeared to be the only food available to the owls during the cold spring nights, ... and were frequently seen in May flying about the forest canopy when temperatures were below freezing" (Reynolds and Linkhart 1987b). Noctuid moths constituted over 70% of the insects (Lepidoptera) captured in light traps by these authors in May and increased to over 90% in September. This increase agrees with Balda's qualitative assessment that noctuids are most abundant in northern Arizona in September and October (Balda *et al.* 1975). Noctuids may be the only prey taxon that is a potential limiting factor for flammulated owls, and they are probably limiting only in May and early June. Goggans (1986) captured no adult Lepidoptera in her traps in May and June, but this may be an artifact of her trap placement and limited number of sample sites. In July and early August she found no significant difference between frequencies of taxa brought to nestlings and those in her insect traps. Numerous other arthropod taxa are also taken (table 2).

Table 2.—Percent composition of diet (and available insects in one case) during summer.

Prey taxon	Oregon ¹	Oregon ²	Various ³	Arizona/ northern Mexico ⁴	Western Great Basin ⁵
Myriapoda					
Chilopoda	4.8	<1	1.4	4.9	
Diplopoda	<1	<1	0.2		
Arachnida					
Scorpionida			3.2	0.8	
Solpugida			0.9	0.4	
Phalangida				0.4	
Araneida	5.9	3.3	4.1	0.8	
Insecta					
Orthoptera	61.9	60.5	19.3	11.4	42.9
Hemiptera			1.6		
Lepidoptera adults	6.3	7.9	36.5	24.4	33.3
Lepidoptera larvae	6.5	<1	9.6	15.4	9.5
Hymenoptera			0.2		
Ephemeroptera	<1				
Diptera				1.2	
Homoptera	<1		1.8		
Coleoptera	<1	14.6	21.4	34.1	14.3
Unidentified /					
Other	11.6	10.3		6.1	

¹Goggans (1986), photographed at nest (n = 352).

²Goggans (1986), traps.

³Ross (1969), stomach contents (n=46).

⁴Marshall (1957), stomach contents (n=27).

⁵Johnson and Russell (1962), stomach contents (n=10).

The assertion that small vertebrates are taken has been repeated for a century without convincing documentation. Smith (1891) took a female whose stomach "contained the remains of some small rodents." Presumably on the basis of this report and the assumption of similarity to other *Otus*, Bendire (1892:375) concluded that "smaller mammals" were a major part of their diet. Bent (1938) concluded the species was "largely, if not wholly, insectivorous, though it may occasionally capture a small mammal or bird." Bent's statement has been repeated in several uncritical compendia. Karalus and Eckert (1974:160) have gone further in asserting that "this owl will eat mice of many varieties, shrews, moles, and, during the nesting season only, a few small birds." It appears that the food habits, as well as the weights, they report are those of the *Otus asio* complex.

In Oregon Bull and Anderson (1978) found a pellet containing the remains of a red-backed vole (*Clethrionomys gapperi*) below a nest tree, and junco feathers in another nest, but the previous occupants, e.g., northern saw-whet owl (*Aegolius acadicus*), may have taken these prey (E. Bull, fide, Cannings pers. comm.). Legs (with bands) of a juvenile mountain chickadee (*Parus gambeli*) were found in a nest in New Mexico; the chickadee had been banded as a nestling 30 m away (McCallum *et al.* in review). Linkhart and Reynolds (in press) found a *Peromyscus* carcass in a nest in Colorado but concluded another species was responsible for killing it. These findings do not demonstrate that the vertebrates were killed or even consumed by flammulated owls, but Cannings (pers. comm.) removed a dusky shrew (*Sorex monticolus*) from the stomach of an apparently healthy (mass = 60 g) owl that struck a window 15 November 1988 in Kelowna, British Columbia. Two unsubstantiated sightings in Montana in 1981, one of an owl perched in a tree with a vole in its talons on 21 November and another of an owl chasing passerines at a bird feeder on 20 December (Holt *et al.* 1987) are likely misidentifications. Nonetheless, the possibility that some flammulated owls overwinter in northern areas by subsisting on vertebrates cannot be completely discounted.

A pair captured by Johnson (1965:101) "died in an emaciated condition after several days in captivity despite nightly consumption of bird carcasses placed in their cage." Captives can be maintained indefinitely on a diet of meal worms and neonatal mice ("pinkies"), but apparently cannot process the bone of mature vertebrates (M. Altenbach, pers. comm.). Captives eat juvenile mice (< 9 g, K. McKaeffer, fide, Cannings pers. comm.), as well as grasshoppers (Richmond *et al.* 1980).

Role of Diet in Species Behavior

As shown by the observations reported by Ligon (1968) and Webb (1982), prey availability is essential to thermoregulation and survival during cold spring nights. This role of diet may in fact determine at least the upper limit of the elevational range occupied by the species (see above). The presumed migratory behavior of the species also appears determined by the seasonal availability of arthropods. The early availability of noctuid moths may therefore advance by up to one month the suitability of North American territories, although this conjecture is untested. Failure to begin nesting in May and early June would require adults to molt while still feeding their young in late summer. They may be able to tolerate such overlap, but it would require more vigorous foraging.

The available data suggest that flammulated owls will forage as readily in grassland/forest edges (Goggans 1986) as in tree crowns (Reynolds and Linkhart 1987b), which results in different primary prey taxa. Unfortunately the relative fitness consequences of these options are not known, and both food studies were of short duration.

Overall, flammulated owls appear to be opportunistic insectivores. As such they are not tied to the population cycles of a particular group of prey taxa. On the other hand their clutch size is quite invariant (see below), and they are unable to increase productivity in response to increased prey abundance in the manner of the boreal owl (Korpimäki 1989), the snowy owl (Parmelee 1992), and the barn owl (*Tyto alba*, Marti 1992). On the other hand, immigration into areas with high prey abundance (e.g. spruce budworm outbreak) is suggested by findings in British Columbia (St. John 1991, van Woudenberg pers. comm.). The response of this species to crashes of prey populations is unknown, and the population dynamics of typical prey species is not well known.

BREEDING BIOLOGY

Phenology of Courtship and Breeding

In North America males arrive on their breeding grounds in late April to early May in southern California (Garrett and Dunn 1981), New Mexico (McCallum *et al.* in review), and Colorado (Reynolds and Linkhart 1987b) and in early May in northeastern Oregon (Bull *et al.* 1990) and British Columbia (Cannings and Cannings 1982). Females, which are inconspicuous before pairing, are thought to arrive later, but pairs have been found at reoccupied nests as early as 3 May (Reynolds and Linkhart 1987b).

Pair Formation

In Colorado pairs remate in the previous year's territory if both return (Reynolds and Linkhart 1987a). Extra-range movements during the previous breeding season serve to acquaint males and females with potential mates if the previous mate does not return. In such cases the male tends to stay on his previous territory and the female to shift territories (Reynolds and Linkhart 1990a). Both these practices tend to shorten and simplify the pair formation process, which allows nesting to begin shortly after the arrival of females. Pairing can take place as late as 8 June (Reynolds and Linkhart 1987a). Mated pairs move through the home range with the male entering and calling from cavities. The female follows the male into cavities (Reynolds and Linkhart 1987b), presumably selecting a nest site in the process. Association of pairs during the winter has not been investigated.

Clutch Initiation and Laying

The southernmost nest recorded in the literature, in Veracruz (328 m), had incubated eggs on 4 April 1939 (Sutton and Burleigh 1940). A female weighing 63.0 g with a 2 mm ovum (indicative of the early pre-laying period) and 6 males in breeding condition were collected in early April in the Sierra del Carmen (Miller 1955). Breeding males were collected south of Ocampo and east of San Antonio de las Alazanas, Coahuila, in April (van Hoose 1955). A nest in adjacent Nuevo León had three incubated eggs on 4 May 1972 (Hubbard and Crossin 1974). An incubating female was taken from a nest in extreme southwestern Chihuahua 15 May 1950 (Stager 1954). Apparently laying is in mid-April, with hatching in May in northern Mexico.

Eggs were laid between 16 May and 4 June in western New Mexico ($n = 11$ eggs from 6 clutches, mean \pm sd = 28 May \pm 5.15) (McCallum *et al.* in review). In Colorado, clutches were completed between 29 May and 14 June ($n = 14$ females, mean = 7 June \pm 4.6). Mid-July fledglings in British Columbia (Cannings *et al.* 1978) require early June laying there. Initiation of nest occupancy (which precedes laying) was on 12 June in Oregon (Goggans 1986).

Repeat nesting and second clutches remain unverified, but fledging dates of 15 and 19 August at one Oregon nest (Goggans 1986) and 16 August in British Columbia (Cannings and Cannings 1982) indicate laying between 1 and 5 July, which is suggestive of renesting. The latter nest was in a box erected on 12 June, > 1 month after arrival of the males, suggesting release from nest-site competition (Cannings and Cannings 1982).

The incubation period is 22 nights in Colorado ($n = 3$ clutches, range = 21-22) (Reynolds and Linkhart 1987b), 23 ± 2 nights ($n = 2$) in Oregon (Goggans 1986), and 24 nights ($n = 1$) in New Mexico (McCallum *et al.* in review).

Eggs hatched between 6 June and 28 June ($n = 13$, mean = 19 June \pm 8.55) in New Mexico (McCallum *et al.* in review), while farther north in Colorado the last egg in 14 clutches hatched between 20 June and 6 July (mean = 29 June \pm 4.6) (Reynolds and Linkhart 1987b). Hatching in a single nest in Idaho was on 30 June (Hayward 1986).

The nestling period averaged 22.9 nights (sd = 2.07, range = 20-26) for 11 New Mexican nestlings from 6 broods, 23.0 for 5 Colorado broods (sd = 1.1, range = 22-24) (Reynolds and Linkhart 1987b), and 22 ± 2 nights ($n = 3$) in Oregon (Goggans 1986). One British Columbia fledgling flew from the nest box 23 nights after its estimated hatching date (Cannings and Cannings 1982).

Fledging occurred between 27 June and 24 July ($n = 14$ birds from 8 broods, mean = 9 July \pm 10.36) in New Mexico (McCallum *et al.* in review), from 13-29 July in Colorado ($n = 14$ broods, mean = 22 July \pm 4.5) (Reynolds and Linkhart 1987b), and from 19 July through 1 August (annual means 26 July ($n = 5$, sd = 7.2) and 28 July ($n = 4$, sd = 4.6)) in Oregon (Goggans 1986). In British Columbia fledglings were on the wing 15-17 July 1977 (Cannings *et al.* 1978) but another fledged on 16 August 1980 (Cannings and Cannings 1982, and see above).

Home Range Size

Home ranges diminished in size during the breeding season in Oregon, from a mean of 15.9 ha ($n = 2$, telemetry points = 81, range = 12.5-19.3) during incubation to 7.9 ha ($n = 5$, points = 320, range = 2.2-12.5) during the nestling period, to 3.6 ha ($n = 4$, points = 126, range = 0.4-7.2) during the fledgling period (Goggans 1986). Linkhart (1984) also noted that home ranges became smaller after fledging, when males spent proportionately more time foraging, but did not quantify this difference. Small home ranges during the nestling period indicate that males are busy foraging and that they reduce the distance traveled to minimize the time between feedings (Goggans 1986). This suggests that foraging habitat around the nest, as well as cavity characteristics, may influence nest-site selection.

Courtship Characteristics

Pair Formation

Unmated males sing throughout the summer at the prehatching rate of mated males (Reynolds and

Linkhart 1987b) and, as in many species of birds, are apparently advertising their single status to unmated females. Returning females presumably re-establish a pair bond with their previous mates shortly after arriving. Unmated females move through territories of males giving food solicitation calls (Reynolds and Linkhart 1987a), but these are not loud and hence not useful for surveys. After pairing they move through the territory, with the male entering and calling from cavities. The female follows the male into the cavities (Reynolds and Linkhart 1987b) and presumably selects the nest site.

Courtship, Feeding, and Copulation

Away from the nest, the male approaches the female silently (McCallum pers. obs.) or while giving faint 2-note hoots (Reynolds and Linkhart 1987b); the female repeats mewing hoots believed to be food solicitation calls. The male perches beside the female and delivers food bill-to-bill. Copulation, when it occurs, follows food transfer. In one case, after a male gave a "location call" (2-note hoot), the female leaned forward in a horizontal position and rocked from side to side before copulation. An intruder male copulated with the same female on the same night without vocalizing (Reynolds and Linkhart 1990a). Mates may preen each other after copulation (Reynolds and Linkhart 1987b). Reynolds and Linkhart (1990a) observed 14 copulations in 17.5 hr of observation during the copulatory period, the first occurring 11 nights before the laying of the first egg.

The rate of allo-feeding of females by males increases to a peak four nights before laying, when female mass is maximal. Both feeding rate and female mass then decrease through incubation. Feeding rates then increase as the male provisions nestlings, but the female continues to lose mass (Reynolds and Linkhart 1987b). McCallum *et al.* (in review) estimated that females lost approximately .5 g per night during this period. Females resume feeding themselves about 12 nights after the young hatch (Reynolds and Linkhart 1987b).

Clutch

Flammulated owls lay clutches of 2-4 eggs, with little annual or regional variation. Mean clutch size \pm standard deviation, sample size, and range for three United States populations are as follows: New Mexico, 2.28 ± 0.49 , $n = 7$, range = 2-3 (McCallum *et al.* in review); Colorado, 2.7 ± 0.47 , $n = 11$, range = 2-3 (Reynolds and Linkhart 1987b); Oregon, 2.7 ± 0.76 , $n = 6$, range = 2-3 (Goggans 1986). Anecdotal records in the literature all indicate clutches of 2-3, except 2

clutches of 4 in Colorado (Smith 1891) and Oregon (Bull and Anderson 1978). Johnsgard (1988) reported a mean of 3.12 ($n = 26$, range = 2-4, 14 clutches of 3) for a geographically scattered sample, mostly from the collection of the Western Foundation of Vertebrate Zoology (WVZ), but some of the latter, including 3 of 4 clutches of 4, were misidentified as to species by the original collectors (L. F. Kiff, pers. comm.). Statistics for authentic clutches at WVZ are mean = 2.83 ± 0.753 , $n=6$, range = 2-4. Only 5 clutches of 4 can be verified, 1 each in Utah (WVZ), Oregon (Bull and Anderson 1978), and British Columbia (R. J. Cannings, pers. comm.) and 2 in Colorado (Smith 1891 and U. S. National Museum).

In Colorado, females lay 2 eggs with inexperienced males, 3 eggs when the males have prior experience. This may be the result of males unfamiliar with their territories providing less food for egg-production by the female, who does not forage during the laying period (R. T. Reynolds, pers. comm.). High male turnover, therefore, may be deleterious to the persistence of a population, even though there appears to be a surplus of males (Goggans 1986, Reynolds and Linkhart 1987a).

Parental Care

Only the female incubates and broods the young. The male brings food to the incubating and brooding female up through about the 12th night of nestling life. Whether he feeds the nestlings directly or the female relays food to them is not known. Both male and female deliver food to the nestlings from the 12th night onward through fledging. The fledgling period lasts 25-32 nights (Reynolds and Linkhart 1987b).

Nest visitation rates are highest just after dusk and before dawn, and variable throughout the rest of the night. Visitation rates differed among four nests studied in New Mexico (McCallum *et al.* in review). Feeding visits are pulsed, and Hayward's (1986) extensive data on one nest suggest that pulses are averaged out such that the nightly total increases monotonically through the nestling stage; thus nests should be monitored all night for accurate representation of nightly rates.

In Colorado, nightly visitation rates peaked midway through the nestling period, which would be about the time the growth rates of the nestlings were maximal (Reynolds and Linkhart 1987b).

DEMOGRAPHY

Demographic modeling allows not only projection (i.e., a prediction of future population increase or decline), but also an assessment of the current status of a population. The Lotka-Euler equation for seasonally breeding species

$$\sum \lambda^{-x} l_x b_x = 1 \quad [1]$$

specifies the effects of age-specific survival probabilities (l_x) and fertilities (b_x , often symbolized m_x) on the (geometric) intrinsic rate of natural increase (λ). If $\lambda = 1$ the population is stationary, neither decreasing nor increasing. (For continuously breeding populations λ^{-x} is replaced by e^{-rx} , and the $l_x b_x$ are integrated instead of summed. The discrete equation also appears in different but mathematically equivalent forms; see Caswell 1989, McDonald and Caswell 1993.)

It would be desirable to estimate λ in these populations in order to assess current trends. Vital rates are, unfortunately, very poorly known for this species. Breeding behavior is fairly well understood, and annual fertility has been estimated in several locations. Otherwise, virtually nothing is known. Below I review the state of knowledge of various demographic parameters, and then use these data in a preliminary demographic model.

Life History Characteristics

Age at First Reproduction (α)

Age at first reproduction is not known. The only bird banded as a nestling ever found breeding had not been recaptured as a yearling, although the territory in which he was eventually recaptured (2.4 km from natal nest) had been occupied continuously since his first year (Reynolds and Linkhart 1990b). It is reasonable to assume $\alpha = 1$ year for females, because females of the much larger eastern screech-owl breed at that age (F. R. Gehlbach pers. comm.). The common existence of unmated territorial males and putative mate-assessment (Reynolds and Linkhart 1990a) suggest that unavailability of mates may force some territorial males to delay onset of breeding for 1 or more years. Both sexes breed annually (Reynolds and Linkhart 1987a).

Annual Fertility and Reproductive Success

One clutch is laid per year. (The two possible cases of late nesting or reneating are discussed above (under Clutch Initiation and Laying). Annual fertility is, therefore, identical to clutch size, which varies between 2 and 4 eggs. Means are 2.28 in New Mexico, 2.7 in Colorado, 2.7 in Oregon, and 2.8 for a sample

from throughout North America (details above under Clutch Initiation and Laying).

Gross fertility is the number of eggs laid. Net fertility can be thought of as the number of fledglings produced. Three independent survival probabilities link these two parameters. The first is the *success rate* of all nesting attempts, that is, the probability that at least one fledgling is produced. Total nest failure can occur at any time between the onset of nesting and fledging because the entire reproductive output is in one vulnerable location. (The likelihood of reneating appears so low for this species that it can be ignored for these estimates.) Nest predators usually destroy the entire contents of a nest, so the effect of nest predation is included in this parameter. Death of either parent before about night 12 (see Phenology) of the nestling period will likely result in starvation of the young, leading to nest failure. The second probability is the *hatching rate* of all eggs in nests that last long enough for hatching to occur. This can be estimated from nests that succeed as well as those that fail completely after the completion of hatching. The final probability is the *fledging rate* of nests that succeed in fledging at least one young. Estimating this probability requires knowing brood size but not clutch size. The product of these three probabilities is the probability that an egg will produce a fledgling. It is permissible statistically to estimate these probabilities from different nests (Lande 1988). Estimating each separately makes it possible to use nests for which data are incomplete. Nest success probabilities from four North American samples are presented in table 3.

The probability of surviving to fledging can be multiplied by clutch size to predict the number of fledglings per nest (table 4). The estimate agrees very well with the average number of fledglings for all nests in the New Mexico data, but not as well for the other three data sets. The study sites represented in these data are reasonably well-distributed geographically, and these data are more extensive than data for other life history parameters.

The number of fledglings produced per nest is often used as an estimate of net annual fertility. When halved (assuming a 1:1 sex ratio) this number becomes b , the age-independent number of female offspring produced per female of breeding age (Leslie 1966, Mertz 1971). Age-specific fertilities are not yet available, but they should be gathered. Age-specific data may show that fertility is age-independent, which would reduce the complexity of demographic sampling in the future.

In Colorado the number of young produced by two inexperienced parents was less than the production

of two experienced parents ($0.05 < P < 0.10$), while pairs with one experienced adult of either sex produced an intermediate number of fledglings (Reynolds and Linkhart 1987a). This difference would be partially reflected if age-specific fertility were available, but it shows that stage-specific (in this case stages would be inexperienced and experienced) modeling may be more useful.

First-Year Survival (I_1)

Although the survival of fledglings to independence is still mainly a parental responsibility, it typically is not included in fertility. It therefore must be included as one of the multiplicative factors in first-year survival. Linkhart's (1984) radio-tracking data yield an estimate of 0.79 for this crucial period, but the predation of several radio-fitted fledglings (Linkhart and Reynolds 1987) by *Accipiter* spp. may have been exacerbated by the extra burden of carrying the radios. The correct figure may be closer to 1.0 (R. T. Reynolds, pers. comm.) for this short but crucial interval.

The probability of surviving the first year is the product of two independent probabilities: survival from fledging to independence (above) and survival from independence to the age of 1 year (at which time breeding presumably commences, see above). The latter probability is unknown for the flammulated owl. None of the > 100 nestlings banded by Reynolds and Linkhart (in press) and the 13 banded by McCallum *et al.* (in review) have returned to their respective study areas in the first or subsequent years after banding. This is typical of young birds (Greenwood 1980) and does not mean they all died. Some fraction must have survived to the age of 1 year in another location, but the size of this fraction is unknown.

It is useful to partition survival from independence to age 1 into two phenologically distinct periods. The first is post-fledging dispersal. It is known that fledglings leave their natal areas earlier in fall than do

adults (Linkhart and Reynolds 1987a), but it is not known how far they go or whether they make the entire trip to their subsequent summer home ranges before or after winter. Radio-tracking a large number of fledglings would make it possible to learn not only survival rates but dispersal distances during the immediate post-fledging period. This will require a study area of 10's of km rather than the more typical 100s of m in perimeter (see Chapter 7).

The second "installment" of post-independence survival is the probability of surviving the winter (including migration) independent of the costs of dispersal. This factor is also unknown for the flammulated owl. It could be obtained by banding juveniles in late summer and early autumn, under the assumptions that natal dispersal is completed before migration and that first-year owls return to the location they left in the previous autumn (Brewer and Harrison 1975). Adults return in exactly this way, so it would be no surprise for yearlings to have the same ability.

Adult Annual Survival

Adult survival has not been estimated with a statistical procedure (e.g., Jolly-Seber, SURGE). A minimum estimate of survival is given by return rates. An estimate of 0.59 was obtained from return rates in the first 4 years of the Colorado study (Linkhart 1984:6). As of 1986 the annual return rate of breeding adults was 8/17 for males and 10/19 for females (Reynolds and Linkhart 1987a) (rates not significantly different: $\chi^2 = 0.111$, $df = 1$, $P = 0.738$). The probability of returning the first year after banding was only 0.38 but increased for subsequent years. Because the first year of banding probably was not the first year of breeding for all these birds, especially at the beginning of the study, survivorship cannot be estimated from these data. An accurate survivorship schedule is gravely needed to assess the viability of this species. It will be difficult to obtain because flammulated owls cannot be aged after

Table 3.—Components of survival from egg to fledging for flammulated owls. Sample sizes are in parentheses.

Source	Nest success	Hatching rate	Fledging rate	Survival to fledging
Colorado ¹	0.88 (58)	0.88 (11)	0.95 (23)	0.74
New Mexico ²	0.82 (12)	0.95 (7)	0.83 (10)	0.66
Oregon ³	1.00 (9)	-	-	0.88 (6)
Various ⁴	0.70 (10)	1.00 (5)	0.91 (4)	0.64

¹Reynolds and Linkhart (1987b).

²McCallum *et al.* (in review).

³Goggans (1986).

⁴Hasenyager *et al.* (1979), Richmond *et al.* (1980), Cannings and Cannings (1982), Bloom (1983).

Table 4.—Predicted (from clutch size and nest success probabilities) and observed fledgling production by flammulated owls. Sample sizes (N) are in parentheses.

Source	Survival to fledging	Clutch size (N)	Predicted fledglings per nest	Actual fledglings per nest (N)
Colorado ¹	0.74	2.7 (11)	2.00	2.3 (26)
New Mexico ²	0.67	2.27 (11)	1.50	1.50
Oregon ³	0.88	2.7 (6)	2.38	2.66 (9)
Various ⁴	0.64	2.80	1.79	1.43

¹Reynolds and Linkhart (1987b).

²McCallum et al. (in review).

³Goggans (1986).

⁴Hasenyager et al. (1979), Richmond et al. (1980), Cannings and Cannings (1982), Bloom (1983).

the first molt of flight feathers, which occurs in late summer after the first birthday as in all *Otus* (Marshall 1967). Aging is most accurate in the first summer, because juveniles retain some of their barred juvenile plumage at least into August, but unfortunately independent juveniles are difficult to find. It may be possible to discern yearlings on the basis of flight feather wear, but this has not been documented. Possible delayed breeding by males makes obtaining a male life table very difficult. Fortunately, male data are not needed for assessing the viability of the population with standard demographic methods.

Lifespan

The maximum lifespan so far detected in the wild is 7 years and 1 month for females, and 8 years and 1 month for males (Reynolds and Linkhart 1990b). True maxima are probably much longer, as these results are based on a small sample. Estimation of average lifespan based on currently available data is not possible because the age at the time of initial capture is not known.

Nonbreeders

Reynolds and Linkhart (1987a) found some territories in which territorial males were present, but no attempt at nesting was evident. These males were believed to be unpaired because they continued to sing through the summer. These males are apparently a surplus and do not contribute to population growth, although their existence would buffer population decline if breeding males but not females were decimated. Nonbreeding females may exist but are unknown.

Geometric Rate of Natural Increase

Because first-year survival (l_1) is unknown, and adult survival is poorly known (although its mean appears ≥ 0.50), it is not possible to calculate λ for any population. The intensive field work required

to estimate l_1 in several locations would be well worth the expense because it would make it possible for the first time to assess viability of populations of this species with some measure of objectivity. In the interim various indirect analyses are available. McDonald (pers comm) has investigated several stage-specific models that generally agree with what follows. What follows is simpler, but involves fewer assumptions. Both analyses are useful.

Assuming that adult survival and fertility do not vary with age, equation [1] may be simplified to

$$\lambda(1-s/\lambda)=lb \quad [2]$$

(Lande 1988), where s = adult annual survival, l = first-year (juvenile) survival (from fledging to age 1), and b = annual fertility. Taking this route, rather than using a projection matrix, eliminates inaccuracies owing to truncation of the life table (Lande 1988) but omits important details, such as the effect of experience on breeding success.

Setting $\lambda = 1$, one may solve for combinations of s , l , and b that ensure a stationary population. Using the 4 net fertilities of table 4 to estimate b , one may ask if values of s and l necessary to guarantee population survival are realistic. The values from table 4 are halved because demographic modeling conventionally treats the number of females in a population. Because b is modeled as the number of fledglings, l is necessarily the survival rate from fledging to age 1. This is the product of 3 probabilities: (1) survival from fledging to independence, which was at least 0.79 in Colorado (see Annual Fertility and Reproductive Success above), (2) successful dispersal, and (3) surviving the winter.

Using the pooled return rate of $18/36 = 0.50$ from data reported by Reynolds and Linkhart (1987a) as a first approximation of s , solving equation [2] for l shows that about 40% of fledglings in the Blue Mountains of Oregon and about 45% in the Colorado population must survive to the age of 1 year in order for the populations to persist indefinitely. Over 60% must survive in the New Mexico population.

These are high numbers; the comparable value for the northern spotted owl is 0.11 (Lande 1988). Return rates are a minimum estimate of adult annual survival, but even if survival is 50% higher than this minimum, yearling survival must be quite high.

Sensitivity analyses (Lande 1988, Caswell 1989, McDonald and Caswell 1993) of these data performed by D. B. McDonald (results to be presented elsewhere) show that λ is generally far more sensitive to changes in adult survival than to changes in other demographic parameters, including first-year survival. In evolutionary terms this means that a species with such low fertility must have very high adult survival in order to persist. In practical terms it means that conserving adults is more important than protecting nests (D. B. McDonald, pers. comm.).

The high sensitivity of λ to adult survival does not mean that fertility is unimportant. Indeed, the survival rates required for $\lambda = 1$ in the New Mexico population appear so high that the plausible explanation is that in fact $\lambda \ll 1$. This deficit could be partially made up if clutch size were increased to the value seen elsewhere in the range of the species (see Clutch Initiation and Laying above). Perhaps the frequent occurrence of 2-egg clutches in this population indicates that most of the birds are inexperienced (cf. Reynolds pers. comm.), a plausible conclusion if pinyon-juniper woodland is suboptimal habitat inhabited mainly by young and/or inefficient birds unable to obtain territories or mates in ponderosa pine forest upslope.

But increases in fertility appear limited in their potential for this species. When compared to the large clutches produced in times of food abundance by snowy owls (Parmalee 1992), barn owls (Marti 1992), and even the smaller boreal owls, at least in Europe (Hayward and Hayward 1993), the small and almost invariant clutches of the flammulated owl do suggest a firm commitment to a conservative, survival-oriented life history strategy. This works well enough for large raptors, but the flammulated owl is small, nonresident, and insectivorous. For this reason, its designation as a sensitive species indeed seems prudent.

Ecological Influences on Survival and Reproduction

The ecology of survival and reproduction have not been studied explicitly. For example, diet has not been correlated with growth of nestlings, although this is a straightforward undertaking, or with overall reproductive success. Home range use has been assessed in two localities (Linkhart 1984, Goggans

1986) but was not correlated with nest success or adult return rate in either case. In part this is because variation in nesting success is low. McCallum and Gehlbach (1988) compared reproductive parameters with habitat measures and found no correlation, perhaps because of low variance in the former. Reynolds and Linkhart (1992) did show that territories in old-growth forest were more likely to be settled than other sites. This implies that reproduction and/or survival is enhanced in old forest, but the hypothesis has not yet been tested. The higher occupancy of the old growth territories still shows the importance of old growth to the viability of the population.

Causes of Death

Egg mortality is minimal. Siblicide and cannibalism are not substantiated, but younger nestlings have been found dead in the nest after fledging of their siblings (McCallum pers. obs., $n = 2$), and one nestling disappeared (McCallum pers. obs.). Starvation apparently occurs during spring snowstorms (Ligon 1968, Webb 1982). One owl apparently died when a large insect became lodged in its throat (Kenyon 1947). Predation is poorly documented but likely given the owl's small size. Nest predation has been documented for the northern flying squirrel (*Glaucomys sabrinus*, Cannings and Cannings 1982) and either a felid or bear (Richmond *et al.* 1980); otherwise, nest predation is unknown. Remains of flammulated owls have been recovered from the stomach of a great horned owl (Johnson and Russell 1962), and Borell (1937) observed predation by a Cooper's hawk. Several fledglings have been killed by accipiters in Colorado (Linkhart and Reynolds 1990a), but maneuverability of fledglings may have been influenced by radio-mounts. Feathers were found on an accipiter "plucking post" near a nest that failed in New Mexico (McCallum pers. obs.). Diseases such as avian pox have not been reported, and feather parasites are very rare.

Social Pattern for Spacing

Estimates of home ranges vary from 5.5-24.0 ha, based on radio-tracking in Colorado (Linkhart 1984) and Oregon (Goggans 1986). Males sing throughout their home ranges, most frequently before hatching. Following hatching most singing occurs late at night. Intense singing bouts occur along the common boundaries of home ranges (before hatching) and sometimes escalate to physical combat (Linkhart 1984), demonstrating the degree of territoriality. Attempted nest-site takeovers have not been observed.

Evidently defense of an all-purpose territory is sufficient to ensure access to nest sites. Silent males occasionally intrude and approach a nest in another territory. The local male vocalizes and sometimes chases the intruder, albeit ineffectively (Marshall 1939, Linkhart 1984, Reynolds and Linkhart 1990a). Territory defense apparently ceases after fledging, for family subgroups disperse without interference at this time (Linkhart 1984).

In Colorado, some territories are contiguous and have long common boundaries (where many interactions occur), but the landscape is not saturated with territories and much space is unoccupied (Reynolds and Linkhart 1987a). Such sites appear suboptimal (Reynolds and Linkhart 1992), but whether they would be occupied if the population were denser is not known.

Territories generally occupy the same space from year to year regardless of occupancy of contiguous territories. Because males do not expand their defended areas when neighbors are absent (with one exception, Reynolds and Linkhart 1990a), it seems unlikely that territoriality depresses viable population size. Rather, territoriality may optimize population size by ensuring that high-quality pairs have the resources they need for maximizing reproduction (Łomnicki 1988).

Local Density Estimates

Population density estimates are of three kinds: (1) nest and occupied-territory counts from intensively studied sites, (2) spot-mapping estimates from intensively studied sites, and (3) call surveys of a more extensive but less intensive nature. The former, of course, provides more dependable data than the latter two methods. Spot-mapping and call surveys are a potentially useful source of information on flammulated owl abundance, but care must be taken in interpreting the data (Reynolds 1987). For example, the owls were said to be "more common than robins" (Kingery 1980) in the Manitou study area in Colorado, on the basis of clusters of singing birds. Subsequent radio-tracking of this population showed that singing owls move widely in their home ranges and that several clusters of song registrations were due to single birds (Reynolds 1987). Call surveys conducted to date have not been calibrated with estimates based on intensive study of a single area. All survey data, then, may suffer from at least three sources of error:

1. The methods used to estimate the area surveyed (the sound or aural envelope) are subject to considerable error owing to wind, topography, etc.

2. Males have been known to travel up to 1 km to answer a tape recorded song (see Goggans 1986), so surveys using recorded calls to stimulate males may overestimate numbers in the assumed study area. On the other hand, not all males sing at all times, so underestimates are also possible.
3. Some males are unmated (Reynolds and Linkhart 1987a), so call counts do not accurately reflect the number of breeding units, which is far more important for demographic analysis than is the number of males.

Population Studies

Table 5 summarizes data from population studies of flammulated owls. Density estimates are calculated by dividing the count of owls (either nests or males) by the size of the study area. Estimates based on the data of Bull *et al.* 1990 are minimal. These authors surveyed a large area incompletely while conducting a habitat study. Nonetheless, their data fall into the population study category.

Spot-Mapping and Equivalent Studies

Marshall (1939) counted 24 males in an area of about 2 square miles, which yields a density of about 1.9 males/40 ha. The area of his study area was not measured, and he called birds actively, so this is a crude estimate. Nonetheless the species was clearly common in this area, as in other locations in the Sierra Nevada of California where 1-night surveys have been conducted (Winter 1974).

Franzreb and Ohmart (1978) conducted a 2-year spot-mapping study of breeding birds of a mixed-conifer site in the White Mountains of Arizona. Their estimates of 10.6 and 10.2 birds/40 ha actually reflect half that many estimated territories. But their study plots were only 15.5 ha, close to the average size of a territory in Colorado (Linkhart 1984). It appears likely that several territories partially overlapped their study site, or that they misinterpreted clusters of song registrations as several males when only one was responsible. Nevertheless, their comparison between logged and unlogged sites is valuable (see below).

Call Surveys

Marcot and Hill (1980) conducted nocturnal surveys for owls in potential timber sale areas in northwestern California. They did not report how they estimated the aural envelope surveyed but reported admittedly crude density estimates of 0.03-1.09 males/40 ha.

Howie and Ritcey (1987) conducted surveys along

roads in the Kamloops region of British Columbia in 1983-1985. They assumed that the detection limit for singing owls was 0.5 km, and they stopped each 0.5 km along routes varying from 3 - 10 km. Density estimates ranged from 0.03 - 0.5 males/40 ha. Clusters of males along one route were estimated at 0.4-0.7 males/40 ha.

In general, densities are not > 1 territory per 40 ha. Exceptions are several sites in the Sierra Nevada of California (Marshall 1939, Winter 1974), where nests were not located and the study area was not measured, and one site in New Mexico (McCallum *et al.* in review), where the estimates were based solely on nests, but home ranges were not mapped. Territories are known to be clumped, so it is possible that the rather small New Mexico study area happened to overlap a local concentration of owls.

Limiting Factors

Limiting factors have not been addressed explicitly in published studies. Nest-site availability is a potential limiting factor, as it is for any obligate secondary cavity nester. Cavities excavated by pileated

woodpeckers and northern flickers are used in the northern part of the range. Farther south, where the pileated woodpecker does not occur, cavity limitation might become serious. Flammulated owls in New Mexico will, however, squeeze into hairy woodpecker cavities (McCallum and Gehlbach 1988) and they typically use sapsucker (*Sphyrapicus*) cavities in Colorado (R. T. Reynolds, pers. comm.). Habitat, especially foraging habitat, may limit population growth more than is currently appreciated (see Metapopulation Structure below).

Patterns of Dispersal

Natal Dispersal

In Colorado, each of five broods averaging 2.8 young fledged over a 2-night period. Young who fledged on the same night associated in subgroups, and the two subgroups separated by the third night after fledging began. One parent attended each subgroup, and they dispersed in opposite directions. As the flight and foraging capabilities of fledglings improved they foraged more for themselves and became independent of parental provisioning by mid-

Table 5.—Breeding densities of flammulated owls based on counts of territories or nests in measured population study areas.

Source	Count	Area (ha)	Number/40 ha
New Mexico ¹			
1982	5	95	2.11
1983	5	159	1.26
1984	2	159	0.50
1985	5	159	1.26
1986	2	95	0.84
Colorado ²			
Minimum estimates from 5-year period			
nests	4	452	0.35
males	6	452	0.53
Maximum estimates from 5-year period			
nests	6	452	0.53
males	9	452	0.80
Oregon			
1984 ³			
pairs	19	1657	0.46
territorial males	27	1657	0.65
1987 ⁴			
nests	13	5270	0.10
callings sites	24	5270	0.18
1988 ⁴			
nests	21	5270	0.16
calling sites	62	5270	0.47

¹McCallum *et al.* (in review).

²Reynolds and Linkhart (1987b).

³Goggans (1986).

⁴Bull *et al.* (1990).

August. Siblings being attended by the same parent roosted close together until mid-August, at which time their roost sites began drifting apart ($n = 1$). They apparently left the study area in late August. Brood division may spread the risk of total brood destruction by predators in that the loud begging of fledglings renders them conspicuous to nocturnal predators and the habit of roosting close together may lead to multiple predation by diurnal predators (Linkhart 1984, Linkhart and Reynolds 1987). Brood division was also recorded by Goggans (1986) in Oregon.

As with most other birds, locally banded nestlings do not return to the study area where they were banded (Reynolds and Linkhart 1990b, McCallum *et al.* in review). This does not necessarily imply that dispersing young travel great distances. Rather, they may travel 5-10 territory diameters like other birds (Shields 1982), which is usually too far to be detected in the study area. One male found 2.4 km (< 6 territory diameters) from its natal nest by Reynolds and Linkhart (1990b) fits this pattern. An exhaustive survey of potential nest sites in a 100 km² area would likely reveal significant information about dispersal of nestlings banded in a typical study area located at the center of the area.

Breeding Dispersal

In Colorado, males reoccupied their previous territories every year they returned, with a single exception. Females were also site-faithful but moved to the adjacent territory to join an unmated male if their mates did not return. In the one case in which a mated male moved, he and his mate occupied an adjacent territory after the resident male disappeared. The abandoned territory had only a few hectares of old forest, while the new one consisted entirely of old growth. Another male expanded his territory to include an adjacent territory that had not been reoccupied (Reynolds and Linkhart 1990a).

In New Mexico, one female used the same nest cavity 3 years, while two females and one male were found in different territories in subsequent years. Otherwise, 18 banded birds neither returned to previously used sites nor were found elsewhere (McCallum *et al.* in review). In Oregon, 5 of 10 territories were reoccupied in the second year of the study, but no cavity was reoccupied (Goggans 1986).

Metapopulation Structure

Winter (1974) reviewed the idea that flammulated owls are "semi-colonial." Several subsequent authors have remarked on finding clusters of calling

owls with large unoccupied (i.e., silent) spaces in between. Caution must be used in discussing this phenomenon, because it is based solely on patterns of calling males and not on locations of nests. Several workers who have sought nests systematically have found them in abundance and not in an obviously clustered pattern (e.g., Goggans 1986, Reynolds and Linkhart 1987a, McCallum and Gehlbach 1988, Bull *et al.* 1990). There are, of course, unoccupied areas in these locales, but the aggregations of territories do not comprise colonies in any sense. Singing males are known to move extensively in response to other singers or to tape recordings (Marshall 1939, Reynolds and Linkhart 1984, Goggans 1986). These clusters, which typically have not been revisited by those reporting them, may be ephemeral aggregations of males engaging in song duels, especially early in the breeding season before females have arrived.

If the phenomenon of clumped distribution of territories is real, and the possibility should not be dismissed peremptorily, it has important conservation implications. Either large areas of suitable habitat are unoccupied, as Winter (1974) concluded or large areas of seemingly suitable habitat are not in fact suitable or are at least are suboptimal (Howie and Ritcey 1987, Reynolds and Linkhart 1992).

Unsaturated Habitat Hypothesis

If suitable habitat is unoccupied the cause is most likely to be found in the demography of the species and/or the landscape mosaic of the region. A long-lived, low-fecundity species will be slow to reoccupy its range after a population decline because its intrinsic rate of natural increase is low. The flammulated owl is such a species (it has a small, invariant clutch and is not known to respond to regional variation in food abundance with nomadism). Current information implies that the flammulated owl is intrinsically incapable of rapid population growth. It is, therefore, a plausible, but perhaps untestable, hypothesis that the flammulated owl suffered a continental population decline in connection with widespread habitat change in the past century. The location of these local clusters of birds, the "semi-colonies" of the literature, may be an artifact of such environmental alteration. Such clusters are especially likely if natal dispersal distances are short, a subject on which little is known (Reynolds and Linkhart 1990b). These clusters may spread and the species may reoccupy all mid-elevation conifer forest in the future. Even if the clusters are not artifacts of habitat alteration but are, instead, evidence of social attraction of nesting pairs (or just territorial

males), the assumption that unoccupied habitat is suitable implies future population growth as colonies spread in extent. This "unsaturated habitat" interpretation of the cluster phenomenon implies that current forest management schemes are compatible with viability and even growth of flammulated owl populations.

Suboptimal Habitat Hypothesis

An alternative interpretation of these putative clusters of flammulated owls is that not all the habitat that appears to humans to be suitable (i.e., similar to occupied habitat) is in fact suitable by the owl's standards. If this is the case then suitable habitat may be saturated, populations are not likely to increase, and current forest management practices may be responsible for forcing remaining owls into enclaves of suitable habitat.

Metapopulation structure has not been investigated intentionally. The phenomenon described above indicates that it should be. Assuming that the owl currently occupies all ponderosa pine forest, or even all old-forest stands may lead to serious overestimation of its total population size.

COMMUNITY ECOLOGY

Habitat Change and Vulnerability to Predation

Logging has been said to increase contact between great horned and Mexican spotted owls, to the possible detriment of the latter (Ganey *et al.* 1986). If opening the structure of the already open pine forests increases the number of great horned owls there, the flammulated owl might also suffer greater predation. Heavy logging may also reduce the attractiveness of a site to accipiters, thereby benefiting the small owls. Fire suppression has resulted in denser forests, often with an emergent overstory (Chapter 5). These conditions may have deterred predators on terrestrial mammals, such as great horned owls. But, they may also offer superior hunting for northern goshawks that prey on Abert's squirrels, and bird-eating hawks. The effect of habitat change on predation pressure is a complex question that has not been addressed in existing research.

Competitors

Other owls are the major potential avian competitors for food, and of them, only the two screech-owls, *O. kennicottii* and *O. trichopsis*, and the elf owl (*Micrathene whitneyi*) take significant numbers of in-

sects. Marshall (1957, 1967) felt that competition was minimal among the species of *Otus*. Range overlap with the elf owl is not great. Some prey species (e.g., grasshoppers, cicadas) are taken by diurnal predators, which might seriously depress prey availability for the owls. Bats, many species of which co-occur with the flammulated owl, are the most likely vertebrate competitors for food, especially in April and May when the diet of owls is dominated by moths. Insect predators and parasitoids may also take a toll on the food supply. None of these possibilities has been studied, but the opportunistic diet selection of the flammulated owl suggests that it is not seriously threatened by food competition, except perhaps in the early breeding season. Nevertheless, population changes in bats may seriously influence population dynamics of this species.

Nest-site competition is a more obvious threat to this obligate secondary cavity nester. Smaller birds (wrens, parids, nuthatches) tend not to nest in the large cavities required by flammulated owls. Birds from the size of bluebirds upward are potential competitors. Owl nests containing bluebird eggs (McCallum pers. obs.) and flicker eggs (Smith 1891) suggest that flammulated owls may evict some potential nest competitors. (An active flicker nest was in the same tree in which Smith found the owl nest containing flicker eggs.) Even if these owls are capable of evicting all passerines and woodpeckers during the early stages of nesting, larger raptors and some mammals are potential nest competitors.

Habitat preferences tend to separate the flammulated owl from other species of *Otus* that are usually found downslope in drier sites. Northern pygmy owls and saw-whet owls are more likely nest-site competitors. Boreal owls are usually found in more mesic forests; nonetheless, four flammulated owl territories in Idaho overlapped boreal owl territories (Hayward and Garton 1988).

As with competition for food, the most serious nest-site competitors may be mammals. Sciurids, such as *Sciurus aberti* in the southwest, *Glaucomys sabrinus* in the northwest (Cannings and Cannings 1982), and *Tamiasciurus* spp. may out-compete owls for nest-sites and also prey on them. Delayed nest initiation, followed by immediate occupancy of a newly erected nest box, in British Columbia suggests serious nest-site competition (Cannings and Cannings 1982). Reynolds and Linkhart (in press) reported seeing a flammulated owl chasing a northern saw-whet owl, which also supports the conjecture that nest-site competition may be serious.

Particular harvest prescriptions may increase overlap of flammulated owls and potential nest-site

competitors. Franzreb and Ohmart (1978) found increases in American kestrels, northern pygmy owls, and northern saw-whet owls, as well as great horned owls, in logged sites in Arizona. Whether these changes are responsible for the absence of flammulated owls from the logged sites is of course unknown, but increased nest-site competition or predation pressure is a possible explanation.

Complex Interactions

Because flammulated owls depend upon woodpeckers for nest cavities and alternate sources of cavity production are rare, the well-being of woodpecker populations is essential to the survival of this owl (and many other species as well). The imperial woodpecker, whose cavities may have been used preferentially in the past, is now absent from most, if not all, of its former range, which broadly overlapped that of the flammulated owl in Middle America. The pileated woodpecker is the preferred source of cavities in Oregon (Bull *et al.* 1990). This species is considered an old-forest species in western North America (although it has expanded into suburban areas in the east). Loss of old forest in the northern part of the owl's range could, therefore, have both an indirect effect (via loss of pileated woodpecker cavities) as well as a direct effect (via loss of preferred foraging and roosting habitat) on the owl's viability. The northern flicker appears to be one of the main excavators of cavities used by the owl south of the range of the pileated woodpecker. This is a common species, but the impact of European starlings (*Sturnus vulgaris*) on flicker populations cannot yet be assessed, as the starling is still in the process of colonizing western mountain ranges. Flickers are indifferent excavators and often reuse old cavities. Starling expulsion of flickers from old cavities (which is rumored to happen) could actually lead to an increase in the number of flicker cavities, if it did not lead to the extinction of local flicker populations.

RESPONSE TO FOREST CHANGE

Stand Scale Response

Logging

Franzreb and Ohmart (1978) studied the effect of timber harvesting on a mixed-conifer forest bird community by comparing densities in harvested and unharvested sites in Arizona. Their spot-mapped densities of flammulated owls (5.3 and 5.2 territories/40 ha) appear unrealistically high, but the ef-

fect of timber harvesting is unmistakable. The unlogged plot had 626.2 trees/ha, 61.1 snags/ha, and 113,984 m²/ha of foliage volume. Comparable figures on the logged plot were 167.7, 21.0, and 15,269.8. Flammulated owls were obviously dense on the unlogged plot, where ponderosa and southwestern white pines provided nearly 80% of foliage volume; they were absent from the logged plot in both years of the study. Loss of nest sites may be the main reason for the difference, but changed vegetation structure cannot be ruled out.

In Oregon, Bull *et al.* (1990) did not find a significant difference between nest sites and unused cavity-bearing trees with regard to logging activity. Nesting or singing owls have also been found in other selectively logged (Hasenyager *et al.* 1979, Bloom 1983, Howie and Ritcey 1987, Reynolds and Linkhart 1987b) or second-growth (Johnson and Russell 1962, Winter 1974, McCallum and Gehlbach 1988) stands. It appears that in British Columbia selective logging is responsible for producing the open-stand structure that characterizes this owl's habitat everywhere it has been studied. Some logging, therefore, may not be detrimental per se, as long as large old trees, open physiognomy, and some dense vegetation for roosting persist.

Clear-cutting, however, apparently renders an area useless for flammulated owls for many decades. Reynolds and Linkhart (1992) have noted that regardless of forest type, all known nests accompanied by habitat descriptions were in or adjacent to mature or old-forest stands. In addition to the obvious connection that old trees are more likely to contain cavities, they may also provide a richer prey base and denser foliage for roosting. Many older second-growth stands may be acceptable to the owls because they were logged without the aid of chainsaws, and hollow trees typically were left standing. Recent practice, however, has been to remove such trees, probably rendering an area uninhabitable for at least 50 years.

Fire

The effects of fire on the species have not been assessed directly. It is known, however, that 20th century fire suppression and the resulting replacement of frequent cool fires with infrequent conflagrations has led to stand structure that did not characterize ponderosa pine forests before European settlement (Chapter 5). The resulting "doghair" stands of stagnant regeneration may provide suitable roosting habitat for flammulated owls, but they probably seriously reduce foraging potential. Grass and small shrubs, which harbor numerous prey species, are

completely shaded out by the dense thickets of stunted pines. The typical foraging maneuvers of the owls may be difficult to perform in close quarters (Reynolds and Linkhart in press). A comparative study of foraging performance and reproductive success in doghair and artificially thinned stands of second growth would help clarify the contribution of fire history to the current status of the owl. Monument Canyon RNA in the Santa Fe National Forest, New Mexico, would be an ideal site for such a study.

Population Response

Although longitudinal studies of the response of flammulated owl populations to forest change have not been conducted, some retrospective analysis may be useful. In the past century ponderosa pine forests in the western United States were subjected first to heavy logging and then to nearly total fire suppression (Chapter 5). How might these activities have affected the owl? Ironically, their ill effects may have canceled each other out. It appears that these owls favor open forest structure for foraging but dense foliage for roosting. Most early logging did not destroy all the trees. The few that remained may have been sufficient in number and size to provide some nesting cavities, but they were not sufficiently dense to allow for safe roosting. As fire suppression led to the establishment of doghair stands under them, adequate roosting sites may have become abundant. This would leave foraging quality as the major determinant of population persistence. This artificial mix of acceptable habitat characteristics is, however, inferior to presettlement forests in at least one respect. Fire suppression eventually leads to conflagrations, which kill all the trees, making large areas as unsuitable for these owls as a clearcut. Nonetheless, management practices that completely eliminate snags and/or doghair in the name of reducing fuel loads may also make an area unsuitable.

Effects of Fragmentation

In general, fragmentation (here I refer to the isolation of quality habitat in small patches) is thought to negatively influence forest interior species by (1) increasing nest failure owing to increased access by edge-associated predators and brood parasites, (2) increasing competition, especially for nest-sites, with edge-associated species, and (3) decreasing dispersal success owing to the dangers of crossing large open spaces. The effects of fragmentation on the flammulated owl have not been studied.

Past research suggests that the flammulated owl is an old-growth species (Reynolds and Linkhart 1992). Old pine forest, however, has an open structure with numerous interior edges. Edges are favored for foraging in both Colorado (Linkhart 1984) and Oregon (Goggans 1986). Moreover, cavity nesters are less susceptible to the increased predation and parasitism associated with fragmentation than are open nesters. Finally, although the risk of crossing openings may be increased by fragmentation, especially for inexperienced juveniles, it should be remembered that the species faces this risk during migration and presumably has evolved a means of minimizing it.

In summary, many flammulated owls live in habitat that is naturally fragmented to begin with. While forest fragmentation should not be ignored as a potential threat to the survival of the species, current information suggests that alteration of *stand* structure within the forest landscape is more deleterious than fragmentation.

Response to Human or Mechanical Disturbance

These owls are very tolerant of humans, nesting close to occupied areas and tolerating observation by flashlight all night while feeding young. Nest abandonment is rare. One female that was dropped 5 m in a weighing bag abandoned its nest but returned to the same cavity the following year (McCallum pers. obs.). The effects of mechanical disturbance have not been assessed, but moderate disturbance may not have an adverse impact on the species. Whether a nesting pair would tolerate selective harvesting during the breeding season is not known.

A sensitivity analysis of life-history parameters by D. B. McDonald (pers. comm.), however, points out that adult survival is probably much more critical to the maintenance of flammulated owl populations than is annual nesting success. McDonald suggests that mechanical disturbance, e.g., thinning or controlled burn, that flushes roosting birds may be a more serious threat to adult survival in October when migrating *Accipiters* may be common than in June, even though the possibility of lost reproduction is obviously greater in the summer.

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Dynamics of Ponderosa and Jeffrey Pine Forests

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FOREST DESCRIPTION¹

Ponderosa (*Pinus ponderosa*) and Jeffrey pine (*Pinus jeffreyi*) forests are ecologically diverse ecosystems. The communities and landscapes in which these trees dominate are variable and often complex. Because of the economic value of resources, people have used these forests extensively.

Humans have greatly altered the structure of ponderosa and Jeffrey pine forests. Heavy livestock grazing, logging, fire exclusion, and climatic events since settlement by Euro-Americans have produced less sustainable forests (Covington and Moore 1994). Comparative photographs from Montana (Gruell *et al.* 1982), South Dakota (Progulske 1974), Colorado (Veblen and Lorenz 1991), Idaho (Boise National Forest 1993), and Arizona (Covington and Moore 1994) provide qualitative evidence that ponderosa pine forests were more open and parklike before the 1920's, with mostly large, mature, and often uneven-aged trees. Dense thickets of seedlings and saplings were rare according to early forest surveys (Ayres 1900, 1901; Beale 1858 as cited in Cooper 1960, Dutton 1887), yet these are a common part of the forest today. Late successional and old ponderosa pine forests now occupy only 2 to 8% of their presettlement abundance in the National Forests of central Oregon (Scientific Society Panel 1993). They have been replaced by dense, multilayered forests that are susceptible to disturbances of historically unprecedented extent and severity (Hessburg *et al.* 1993, Lehmkuhl *et al.* 1993, Covington and Moore 1994). Habitat has changed for the many bird, mammal, reptile, and amphibian species that live in ponderosa pine forests (Thomas *et al.* 1979b, Patton 1988). Scientists concerned about the ecological status of ponderosa pine forests and the large decline in the extent of old forests have called for ecological restoration of these ecosystems (Mutch *et al.* 1993; Covington and Moore 1992, 1994; Everett *et al.* 1994).

The vast literature on ponderosa pine forests reflects their extensive range, varied composition, and variety of uses. The ecology and management of ponderosa pine forests has recently been summarized by Baumgartner and Lotan (1988) and Lotan and Morgan (1993); both include extensive literature citations. Silvicultural recommendations for different regions are provided by Barrett (1979, 1980), Alexander (1986, 1987), various authors in Pearson (1950), Burns (1983), Schubert (1974), Thomas (1979), and others.

Forest Extent

Ponderosa pine forests are found on more than 60 million acres in the western United States (Oliver and Ryker 1990; see Map 1 for combined ponderosa and Jeffrey pine distributions). The species is often an early seral species in mixed conifer forests but is the climax tree species on drier sites. The elevational and moisture conditions where these forests are characteristically found vary geographically (figure 1) (Barbour 1988, Peet 1988). Warm, dry summers and cold, wet winters are typical. Ponderosa pine is one of the most widely distributed and economically important pines in western North America (Oliver and Ryker 1990).

Jeffrey pine is found primarily in the Coast Range and Sierra Nevada mountains of California but also occurs in southwestern Oregon and western Nevada. Jeffrey pine is especially drought tolerant and cold hardy, suiting it to dominate on harsh, infertile sites (figure 2). Jeffrey pine resembles ponderosa pine in appearance (Jenkinson 1990).

Landscapes, Communities, and Stands

Over an extensive range, ponderosa pine forests are found in a variety of environments and across

¹ Most of the information presented here is drawn from the extensive literature on ponderosa pine because the few studies of Jeffrey pine ecology are mostly limited to northern California (Jenkinson 1990). Because the two species are similar, and ponderosa pine occurs in many of the forests where Jeffrey pine is found (Barbour 1988, Jenkinson 1990), the information included here will likely apply to Jeffrey pine forests as well.

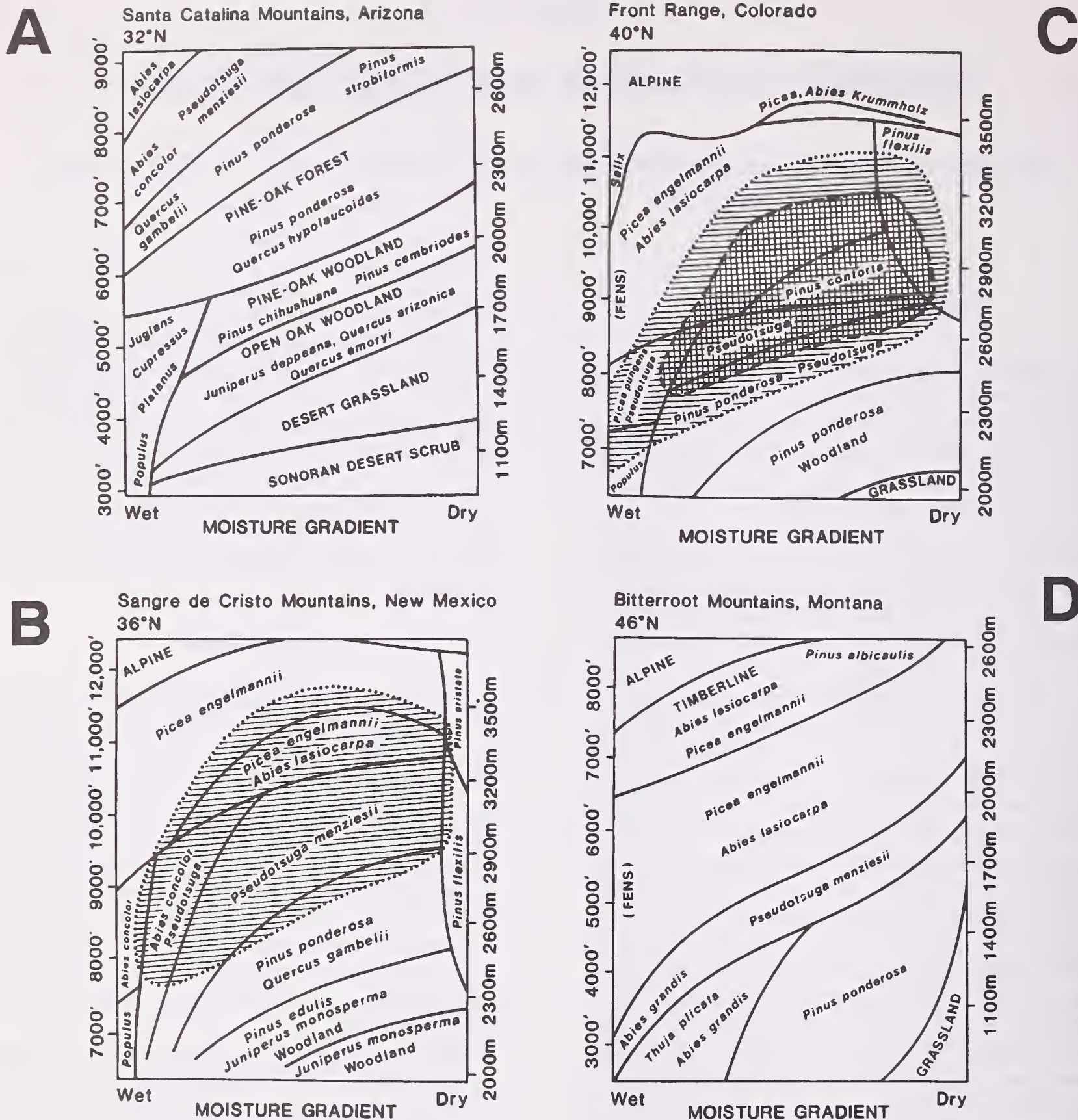


Figure 1.--Ponderosa pine forests occupy mostly dry, low to mid-elevation sites, but the distribution varies geographically. These gradient mosaic diagrams illustrate variations in vegetation compositions with elevations and topographic positions for 4 sites along a latitudinal sequence. In B and C, the shading down to the left indicates the range of *Populus tremuloides* as an important post-disturbance species, whereas shading down to the right indicates the range of *Pinus contorta* as an important post-disturbance species (from Peet 1988).

land ownerships with strikingly different management objectives. The genetic variability in ponderosa pine is also great. The two recognized varieties, Pacific ponderosa pine (*Pinus ponderosa* var. *ponderosa*) and Rocky Mountain (*P. ponderosa* var. *scopulorum*) differ, and there is significant genetic variation within and between stands (Rehfeldt 1986a, 1986b, Conkle and Critchfield 1988, Linkhart

1988a,b). As a result, fire frequency, tree regeneration success, relative growth rates of trees, tree susceptibility to diseases and insects, and potential forest productivity for timber, wildlife, and other uses vary with geographic location, soil type, and stand conditions throughout the range of this species.

The natural diversity in stand and landscape structure has been augmented by past logging, diseases,

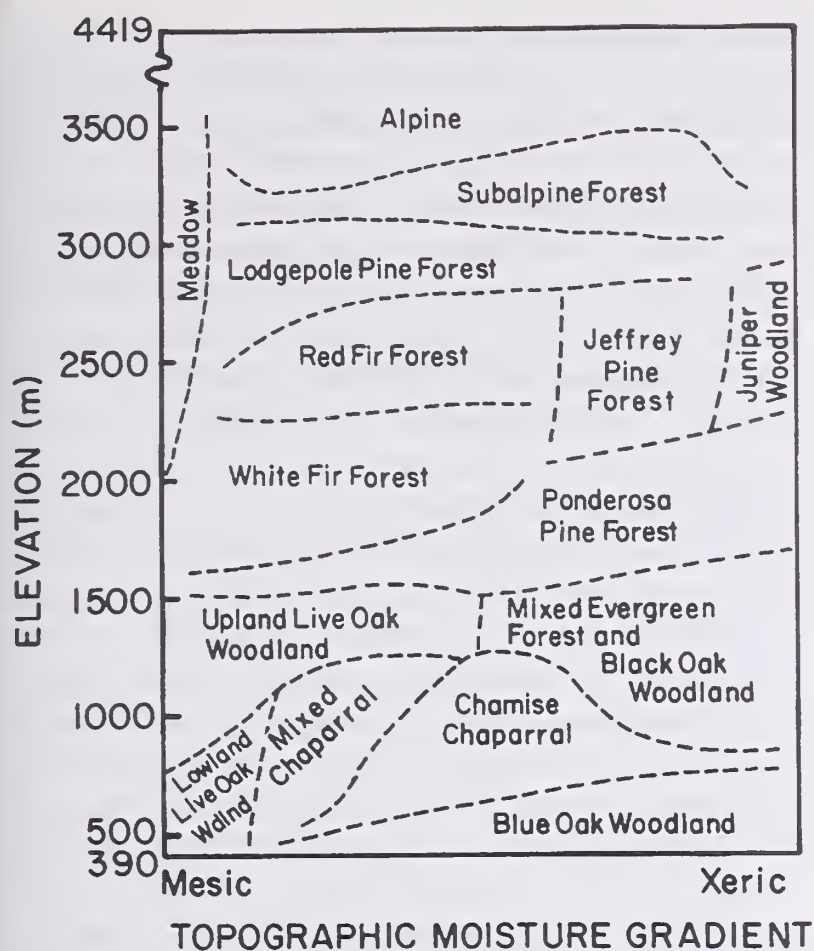


Figure 2.--Jeffrey pine occurs in ponderosa pine forests but is also found in mostly pure stands on drier, more severe sites (from Barbour 1988).

insects, and fires. Ponderosa pine forests vary in stand density, age class distribution, tree vigor, presence of diseases and insects, and patchiness. Both ponderosa and Jeffrey pine trees can occur in dense thickets or in open parklike stands with an understory of bunchgrasses or shrubs. Both species form extensive pure stands or occur as seral dominants in a mixture with other conifer tree species. Both tree species are intolerant of shade and stagnate in dense stands; sapling densities may be as high as 42,000 stems per hectare (Jenkinson 1990). Even in open stands, tree boles are ordinarily clear of branches for much of their lower half. As trees age, the crowns change from short and conical to flat-topped (Harlow *et al.* 1991). In mature trees, branches are large and the foliage is predominately on the outside of the crown where it is exposed to higher light intensities. This structure is well-suited to birds that perch or feed within the crown; the crowns of large trees can shelter birds and insects from weather. The trees have deep tap roots and many lateral roots that extend horizontally at moderate depths through surface soils, often beyond the extent of the tree crown.

Forests are typically patchy, usually structured as groups of 3 to 44 trees of similar diameter (White 1985). Although Cooper (1960) found that groups of trees were of similar age, more detailed analysis on

an unharvested site near Flagstaff, Arizona, showed that ages of trees within the 0.1 to 1.7 ha groups differ by 33 to 268 years (White 1985). On similar sites in Arizona, patches varied in size from 0.03 to 0.26 ha, averaging 0.06 ha (Cooper 1960, White 1985, Moore *et al.* 1993). Where ponderosa pine is a seral species, stands may be even- or uneven-aged. Trees growing where ponderosa pine is the climax dominant are usually uneven-aged. Multiple canopy layers are common, although parklike forests with a single tree canopy layer and a continuous sward of grasses, forbs, and shrubs are also common (Everett *et al.* 1994). Tree regeneration is sporadic, but generally more reliable on the more mesic sites where ponderosa pine is seral. Tree-ring studies indicate that in the past, successful tree establishment was infrequent and depended on a favorable combination of fire or other disturbance to reduce competition from herbaceous vegetation; climate, including spring moisture and little frost heaving (Pearson 1923); reduced competition with grasses and shrubs; and a favorable seed crop. Seed production varies greatly from year to year (Schubert 1974, Barrett 1979).

Understory vegetation in ponderosa pine forests varies greatly in structure and composition. Typically, diverse communities of perennial grasses, forbs, and/or shrubs form in tree canopy openings and where tree density is low. Trees affect productivity of the herbaceous vegetation, which in turn affects the abundance of many insects and wildlife species. When trees are dense, less light and nitrogen are available (Moir 1966), and nitrogen accumulates less rapidly (McConnell and Smith 1970). Most of the herbaceous vegetation is found in the interspersed meadows and openings. Herbaceous production declines sharply as tree basal area and therefore canopy cover increases (figure 3). Few grasses, shrubs, or forbs are found where the tree overstory is dense.

The plant communities associated with climax and seral pine forests are described by authors of the various habitat type, plant association, and community type classifications. Many authors also include extensive information on management, productivity, and successional relationships. Lotan and Morgan (1994) list such classifications for ponderosa pine forests.

Ponderosa pine forests are mosaics of meadows, riparian areas, shrublands, and woodlands intermixed with pine trees. Forest landscapes are a complex of communities with open grassland parks, mixed with dense stands of trees and meadows; all are often mixed with other forest, shrub, and wood-

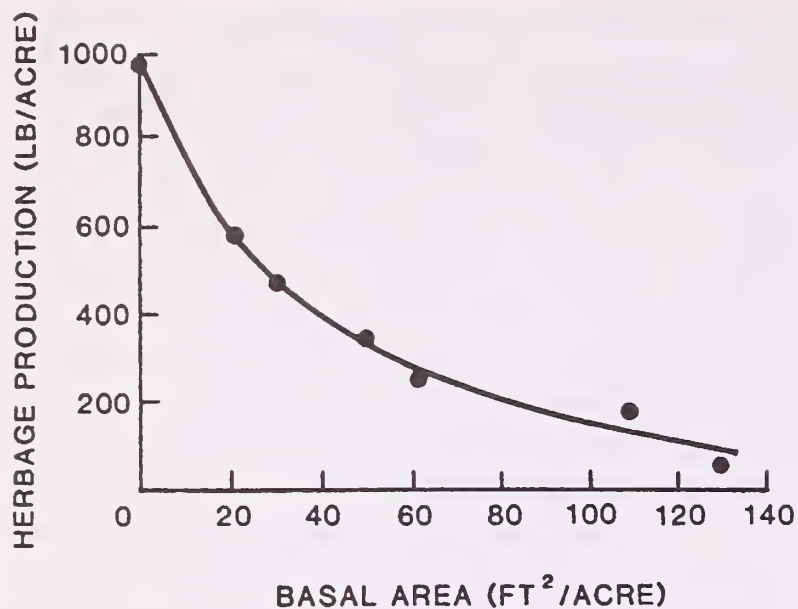


Figure 3.--Productivity of the herbaceous understory vegetation declined sharply as overstory tree density increased in Arizona. Production was greatest in open stands, in thinned stands and in forest openings (from Clary 1975).

land types where topography is complex. The diverse structure of the forested landscapes provides habitat for diverse plant, animal, and insect species.

HUMAN USE OF FOREST RESOURCES

People value ponderosa and Jeffrey pine forests for timber and other wood products, forage for domestic livestock, wildlife habitat, recreational opportunities, watershed protection, and spiritual and aesthetic values. Today and in the past, the ponderosa pine zone is the most heavily used forest zone in Colorado (Myers 1974) and elsewhere. Human use occurs year-round, varying from recreation, residential, and wood production, to wildlife habitat and livestock production (Myers 1974).

Many ponderosa and Jeffrey pine trees were harvested in the early 1900's to support human settlement. Many thousands of hectares were harvested for fuel, mining timbers, railroad ties, and lumber during the late 1800's in the Rocky Mountains (Alexander 1986, Schubert 1974, Steele 1988), in the Pacific Northwest (Barrett 1979), and in California (Oliver and Ryker 1990). To meet market demands, the large-diameter ponderosa pine were often high-graded from the forests with little attention to what was left. Extensive burning accompanied early mining, logging, and railroad construction (Gruell *et al.* 1982). The combination of harvesting and burning was sometimes severe enough to greatly prolong vegetation recovery. Grazing by domestic livestock was extremely heavy in the early 1900's and during World War I (Oliver *et al.* 1993). Disease, insects, and fires have also influenced stand structure and composition.

Today, many state and local economies in the western United States benefit from the harvesting and manufacture of wood products from ponderosa and Jeffrey pine. For instance, half of the economic base in some counties in eastern Oregon is derived from ponderosa pine industries (van Hooser and Keegan 1988). Ponderosa pine contributes significantly to the timber sector of the economies of northern California, Washington, Idaho, Montana, New Mexico, and Arizona; in the latter two states ponderosa pine is the species most often harvested (van Hooser and Keegan 1988). The nontimber uses of ponderosa and Jeffrey pine forests, including grazing, recreation, watershed protection, tourism, and hunting, also contribute significantly to local economies.

Humans have long used ponderosa pine forests. American Indians often purposely and inadvertently ignited fires to facilitate travel; to improve hunting; to enhance production of desirable food, medicine, and forage plants; and for communication (Barrett and Arno 1982). The distribution and structure of ponderosa pine forests were partially determined by fires ignited by lightning and American Indians (Gruell 1983).

Wood Products

Ponderosa pine is widely harvested. The value and volume of its lumber make it one of the most important lumber species in the interior west and one of the most important western coastal tree species (Blatner and Govett 1988). Harvesting and processing the lumber and wood products from ponderosa pine contributes substantially to the state and local economies of the western United States; about 35,000 people are employed each year (van Hooser and Keegan 1988). In the 1920's partial cutting was common throughout the Rocky Mountains (Schubert 1974, Gruell *et al.* 1982, Oliver *et al.* 1993). Clearcutting and partial cutting have predominated since the 1960's, particularly in the Pacific Northwest (Oliver *et al.* 1993).

Timber harvesting to meet the much greater demand for large-diameter logs has contributed to the dramatic change in forest structure. The most valuable wood products come from large-diameter logs (Ayer-Sachet and Fahey 1988). The moldings and frames for doors and windows cut from the outer shell of large logs with few knots command the greatest prices. Plywood is also cut from large-diameter logs. When trees are of small diameter and have lots of branches, the logs are small with lots of knots and yield much less valuable wood. Such logs are processed into dimension lumber, particle board,

house logs, posts and poles, firewood, or wood pulp for paper; these logs also produce the majority of the chips, sawdust, shavings, and bark byproducts. As the large-diameter trees with few branches on the lower stem cut from old forests become fewer and/or less available, they will become even more valuable.

Grazing, Wildlife, Water, and Recreation Resources

Extensive and valuable forage in ponderosa pine forests supports an important livestock industry (Skovlin *et al.* 1976). Many palatable shrubs and grasses grow in ponderosa pine forests. Grazing capacity varies from 0.8 to 6 hectares per animal unit month (Clary 1975, Currie 1975). The dense stands provide shelter from summer sun and winter storms. Openings between stands produce twice as much forage and are used more than forest stands (Skovlin *et al.* 1976).

Cattle and sheep grazing was extensive and heavy early in this century. Increasing rapidly from about 1880, the number of sheep grazed peaked in the 1920's and 1930's (Oliver *et al.* 1993). Heavy grazing by cattle started before 1900 and continues into the present on many sites (Oliver *et al.* 1993). This heavy grazing reduced fine fuels that carried fires and contributed to less frequent fires in the last century in many ponderosa pine forests. Madany and West (1983) implicated livestock grazing as a primary factor influencing alteration of ponderosa pine forest structure since European settlement in Utah.

Many wildlife species use ponderosa pine forests. Patton (1988) estimated that more than 275 bird and mammal species use these forests seasonally or year-round. In the Blue Mountains of Oregon and Washington, ponderosa pine forests provide feeding habitat for 154 species and reproducing habitat for 112 species of reptiles, amphibians, birds, and mammals (Thomas *et al.* 1979b). In comparison, 148 species feed and 129 species reproduce in mixed conifer forests; 106 feed and 84 species reproduce in grand fir forests (Thomas *et al.* 1979b).

Wildlife species are important in the functioning of ponderosa pine ecosystems. Many snag-dependent wildlife are insectivorous and probably limit the size of insect populations, at least at endemic levels (Thomas *et al.* 1979a). Many small mammals and invertebrates within forests influence ecosystem dynamics. For instance, Skinner and Klemmedson (1978) showed that approximately 6 kg/ha/yr more nitrogen is returned to the forest floor via feeding debris from squirrels feeding in pine trees in com-

parison to trees where there are no squirrels feeding. Many small mammals feed upon the mycorrhizal fungi and distribute the spores of the fungi in the Southwest (States 1979 cited in Patton 1992) and the Pacific Northwest (Maser and Trappe 1984). Where grass and shrub understory productivity has declined, this has significantly degraded the habitat for insect, small mammal, and songbird species dependent upon that vegetation for hiding and feeding.

Ponderosa pine forests produce only small to moderate amounts of water as stream runoff. Watersheds can be managed to increase water yield for downstream use, alter the timing of runoff, reduce erosion and sedimentation, or control flooding, but the yields are low (see review by Lotan and Morgan 1993).

Opportunities abound for year-round recreation in ponderosa pine forests; these forests are used extensively for hiking, skiing, camping, bird watching, and other recreational uses. Open park-like stands with scattered large trees and an abundance of grass and shrubs are aesthetically pleasing (Schroeder and Daniel 1981, Brown and Daniel 1986), particularly where they are mixed with meadows, riparian areas, and occasional dense stands.

PRESETTLEMENT FORESTS

Many forests were once ponderosa pine savannas (Dutton 1887; Beale 1858 in Cooper 1960; Biswell 1973), with a discontinuous overstory of scattered, large pine trees and a diverse and extensive understory of perennial grasses and shrubs -- features identified as important to flammulated owl foraging ecology (Chapter 4). Weaver (1974) quoted C.E. Dutton's description of ponderosa pine forests of northern Arizona in the 1880's: "The trees are large and noble in aspect and stand widely apart... Instead of dense forests, we can look far beyond and see the tree trunks vanishing away like an infinite colonnade." Early historical descriptions, including maps and photographs, of forests in the northern Rockies are found in Leiberg (1899, 1900), Ayres (1900, 1901), and similar early forest surveys from throughout the western states. Leiberg's (1899, 1900) photographs of ponderosa pine forests are of open, parklike forests with bunchgrass or shrub and grass understories, with scattered snags, logs, and pines. Ayres (1900) found ponderosa pine forests were "very open and easily navigated on horseback."

Now, such forests have well-developed understories of young ponderosa pine or are codominated by Douglas-fir, grand fir, and other trees that are less

fire-resistant or produce less valuable lumber than ponderosa pine and Jeffrey pine. Extensive changes in forest structure have been documented throughout the Southwest (Cooper 1960; Gruell *et al.* 1982; White 1985; Covington and Moore 1992, 1994), in Montana (Habeck 1990, Arno and Scott 1993), in the Pacific Northwest (Barrett 1979, Everett *et al.* 1994), Idaho (Steele *et al.* 1986, Barrett 1988), Utah (Madany and West 1983), Washington (Weaver 1959), and California (van Wagtendonk 1985, Laudenslayer *et al.* 1989). Barrett (1979) estimated that within the last 25 years other conifers have replaced ponderosa pine as the dominant overstory species on over 2 million hectares in the Pacific Northwest. Tree establishment peaked in the 1920's in southern Utah (Madany and West 1983) and in Arizona and New Mexico (Arnold 1950). The ratio of trees less than 100 years old to those greater than 100 years old was 15 times greater where livestock grazing was extensive (ratio 11.0) than on a similar site inaccessible to livestock (ratio of 0.7) (Madany and West 1983). Pearson (1950) estimated that two-thirds of the ponderosa pine trees currently living in the Southwest were established about 1920 as the result of livestock grazing, increased spring precipitation during an otherwise droughty period, and an abundant seed supply.

As tree density increased, perennial grass cover declined. Arnold (1950) documented grass cover reduction to 25% of what it had been in 1911, 39 years earlier. Livestock grazing was a critical factor in tree establishment (Madany and West 1983), although drought and decreased fire frequency also contributed. Perennial grasses compete with pine seedlings for moisture and have an allelopathic effect on germinating tree seedlings (Jameson 1968). Madany and West (1983) compared grazed and inaccessible sites in southern Utah. They found few thickets of young pine in ungrazed stands and attributed the dramatic contrast in stand structure to heavy livestock grazing in the early 1900's. Although fire exclusion would eventually have a similar effect, the conversion of savanna into forest was enhanced with livestock grazing. Grazing also reduced fine fuels and contributed to the decline in fire frequency in the late 1800's shown in many fire history studies.

Covington and Moore (1992, 1994) simulated changes since settlement for ponderosa pine forests in Arizona. Tree density increased from an average of 23 trees/acre in presettlement forests to 832 trees/acre today. Today, basal area is 4-7 times higher, crown closure has increased by 3-7 times, fuel loading is about 9 times greater, and herbage production is 4-9 times less than on the same sites 100 years earlier. Today, most of the trees are less than 4 inches

in diameter (Covington and Moore 1994). Forest structure changed from an open pine savanna with abundant grasses to dense forest, a condition which likely provides lower-quality flammulated owl foraging habitat (Chapter 4).

Paleoecology

The recent changes in composition and structure of ponderosa pine forests remind us that forest structure is dynamic on several temporal and spatial scales. Mehringer (1985) and others describe the shifts in vegetation composition over millennia documented through studies of pollen and macrofossils from bogs and pack-rat middens. These changes reflect the lack of long-term permanency of vegetation associations (Mehringer 1985, Habeck 1988). Studies of pollen and other evidence of past climate suggest that during the Holocene epoch, 4,000 to 8,000 years ago, species migrated northward by 500 to 600 km (Wells 1983) and upward in elevation (Mehringer 1985) in the Rocky Mountains and Great Basin. Ponderosa pine was relatively scarce in the Southwest during the last glacial period. In the Southwest, vegetation zones have migrated 900 to 1,400 m upward since the last glaciation 12,000 to 14,000 years ago (Hall 1985). There, climates were extremely dry and warm 5,000 to 7,000 years ago (Hall 1985). Changing ratios in the abundance of charcoal and pollen reflect changing fire regimes in the Holocene epoch (Mehringer 1985).

Historical Fire Regimes

Since 1900, fires have been less frequent and more severe in ponderosa pine forests throughout western North America (Arno 1988, Steele *et al.* 1986, Barrett 1988) in both wilderness and areas subject to intensive management. In the Southwest, where fires were typically 1,200 ha in size prior to 1900, some fires now reach 4,000 to 8,000 ha (Swetnam and Dieterich 1985, Swetnam 1990). Crown fires were extremely rare or nonexistent prior to 1950 in the southwestern United States (Cooper 1960). Today, the likelihood of crown fires is increasing. Large, severe wildfires have become common throughout the range of ponderosa pine, suggesting that human activity, including fire exclusion efforts, have changed the fire regime to one of large fires burning in heavy fuels (Arno and Brown 1991). In comparison to surface fires, crown fires are far more difficult to suppress, more threatening to human life and property, and where unprecedented, are more damaging. Stand replacement fires which cover more

than a few acres remove flammulated owl habitat, and, depending on successional patterns, that habitat may be removed for decades to centuries.

In low-elevation forests, historical fires were typically nonlethal surface fires that burned large areas but killed few large trees. On more mesic sites, including those at higher elevations and many sites where ponderosa pine grows but other trees are climax, fire effects were more complex and variable. Fires occurred at longer intervals (40 to 150 years) in a mosaic of nonlethal understory and lethal stand-replacing fires (Arno 1980). Many patches also remained unburned as the fires spread where fuels, topography, microclimate, soils, and changing weather and fuel moisture were conducive. These fire regimes created and maintained a heterogeneous landscape.

Prior to 1900, low-intensity surface fires burned ponderosa pine forests every 1 to 30 years, at least since 1500, and probably since the last glaciation (Arno 1988). Fires were frequent in both seral and climax forests. Flammable fuel accumulated as needles and branches fell and as trees, shrubs, grasses, and forbs grew. The long needles with their high surface-area-to-volume ratio dried out quickly, creating a porous fuel bed. Surface fires spread easily, particularly in open stands with continuous grass or shrub layers.

In the Southwest, fires occurred every 2 to 12 years in the 1700's and 1800's (Cooper 1960, Dieterich 1980, Swetnam and Dieterich 1985) and were more frequent than in eastern Oregon where the mean interval between fires was 25 to 40 years (Hall 1976). In eastern Washington, fire-free intervals varied from 6 to 47 years (Weaver 1959, 1967). In western Montana, Arno (1976) documented average intervals between fires of 6 to 10 years in climax ponderosa pine stands and 7 to 19 years where ponderosa pine is seral to Douglas-fir. In Jeffrey pine forests and mixed conifer forests, mean intervals between fires prior to 1875 were 8 years in pine-dominated sites and 16 years in more mesic sites dominated by true firs (Kilgore and Taylor 1979). Barrett and Arno (1982) compared fire scars on trees from environmentally similar sites that differed in use by American Indians in Montana. Fires occurred twice as often on valley bottom and lower elevation sites that were heavily used by American Indians. Chronologies indicate similar fire intervals back to 1500 (Barrett and Arno 1982).

As Europeans arrived, prospecting, mining, land clearing, railroad building, and other human activity led to a major increase in fire frequency during the late 1800's (Arno 1980). Fire frequency has de-

clined dramatically since then as livestock consumed the grass that fueled many fires, roads created fuel breaks, cultivation and settlement of the valleys limited fire spread there, and periodic burning by American Indians ceased. Fire suppression became increasingly well-organized and efficient between 1900 and 1930 so that by mid-century, most fires of low to moderate intensity could be extinguished (Agee 1990). Due to logging and mining-related activities and fewer fires, fuels accumulated, leading to more intense and more destructive fires.

Steele *et al.* (1986) found that severe fires became more common after 1895 in the ponderosa pine/Douglas-fir forests of central Idaho. Fire frequency decreased, from an average of 10 to 22 years between fires prior to 1895 to only occasional fires since then. Agee (1990) calculated that 210,000 hectares of ponderosa pine forests burned each year prehistorically in Oregon. This is equivalent to about 7% of the range of ponderosa pine forests in Oregon and is far above the area that burns now either in wildfires or prescribed fires, even in years in which fires are very extensive (Agee 1990). In Montana, Habeck (1990) suggested that the size and severity of fires affecting two separate parts of an old remnant forest in 1977 and 1985 were the consequence of no fires occurring since 1918 where fires had once occurred every 7.1 years from 1557 to 1918. No fires occurred until 1977 and 1985, when severe fires killed most trees on two separate slopes.

Old-Growth Forests

Old-growth forests have important biological and social values. They are habitat for a variety of animal, plant, and insect species and can provide long-term biological records of climate. Socially, they are valued for the economic value of some large-diameter trees, for recreation, and as part of our natural heritage. "Old growth" is variously defined by ecological (structure and function), social (lack of harvest or other evidence of human use), wildlife habitat (stand structure), and forest planning (age or size structure) criteria (Hunter 1989, Hayward 1991, Kaufmann *et al.* 1992). Given the controversies associated with describing old growth, the term old-growth here refers to those forests that fit Hunter's (1989) criteria that species composition has stabilized, average net annual growth is close to zero, growth rate is below the lifetime average, the forests are significantly older than the average interval between stand-replacing disturbances, dominant trees are at least as old as the average life expectancy for the species on the site, forests have not been

intensively or extensively cut, and people have never converted the forests to another type of ecosystem. Typically, snags, canopy gaps, and multiple tree canopy layers are present, and shrub, herb, and grass species are relatively abundant; these conditions appear favorable to flammulated owls (USDA 1992).

Old forests are inadequately represented in the landscapes of eastern Oregon and Washington according to Everett *et al.* (1994). They summarized the data of Lehmkuhl *et al.* (1993); who estimated the extent of old, mature, and parklike ponderosa pine and Douglas-fir forests currently (1985 to 1990) and in the past (1932 to 1959) in six river basins. The percentage of the total area occupied by old forest declined by 52-82% in 4 of the 6 watersheds (Lehmkuhl *et al.* 1993, Everett *et al.* 1994). Old forests increased in one watershed by 26% and did not change in another watershed.

Some characteristics of old forests occur where multilayered canopies have developed recently in mature forests. However, where those canopy layers have developed and shade-tolerant species have established in abundance, the associated risk of loss to fire, insects, and disease is higher than in old forests (Lehmkuhl *et al.* 1993). Increasing continuity of species and structures increases the potential extent and severity of damage (Hessburg *et al.* 1993).

It is difficult to find old ponderosa pine forests that have not been influenced by fire exclusion, grazing, timber harvest, or other management. The ecological status of small remnant forests is affected by the management in surrounding forests to such a degree that the ecological value of the old forests may be compromised. Moir and Dieterich (1988) stated that most of the old ponderosa pine forests in the Southwest were deteriorating due to fire exclusion.

If we understood the structure and ecological processes in old forests, we could use that to guide management. An understanding of the historical range of variability in ecosystem structure can be used to guide management (Swanson *et al.* 1993, Morgan *et al.* in press). It is particularly useful for understanding the processes of old forest development, but an understanding of the range in abundance and pattern of old forests would be helpful both in defining the range of desired future conditions and the limits of acceptable change (Morgan *et al.* in press), and to define the conditions that flammulated owls occurred in prior to industrial influence.

Covington and Moore (1992, 1994) warn that defining old-growth forests based upon current conditions within old remnant forests may not be "compatible with the natural conditions prevalent throughout the evolutionary history of the organisms living in western forests." They argue that we

must reconstruct past forest structure based upon detailed analysis of the age of trees within current stands. They were particularly concerned that current conditions are decidedly unnatural. In addition, we must consider the extent to which snags and downed woody debris were abundant prior to settlement.

Based on analysis of the age of trees of presettlement origin, canopy cover varied from 17 to 22% (White 1985, Covington and Sackett 1986) in the Southwest. Pearson (1923) noted that ponderosa pine canopy cover seldom exceeded 25%. Density varied from 7 to 62 trees/ha in Utah (Madany and West 1983) to 52 to 148 ponderosa pine growing with 8 to 129 Douglas-fir trees/ha in 8 stands in Montana (Arno and Scott 1993). Several different sites have been studied in Arizona where estimates of tree density regenerating prior to European settlement vary from 32 trees/ha (White 1985), to 57 to 138 (Covington and Moore 1992) and 86 to 111 trees/ha (Cooper 1960). In all cases, current tree densities are 2 to 37 times this number (Cooper 1960, White 1985, Covington and Moore 1992, Arno and Scott 1993). Habeck (1990) analyzed the size structure of remnant old ponderosa pine, Douglas-fir, and western larch forests near Missoula, Montana. He found an average of 32 and 67 trees/ha greater than 50 cm dbh (diameter at breast height) on warm, dry habitat types on south slopes and cool, moist sites on north slopes, respectively. He estimated that in 1900 these sites supported 93 and 172 trees/ha; today, total tree densities on these sites average 2,296 and 1,906 trees/ha (Habeck 1990).

The structure of old forests reflects the episodic nature of regeneration (Cooper 1960, White 1985, Habeck 1990, Arno and Scott 1993). Within stands, successful establishment was infrequent and episodic, with as many as 40 years between regeneration events. However, regional precipitation patterns favored simultaneous regeneration over large areas (Covington and Moore 1992, Swetnam 1990).

Snags are valuable to many wildlife species as nest and roost sites, as posts for hawking, singing, and perching, and as a feeding substrate (Cunningham *et al.* 1980). Many insect larvae invade recently dead trees (Keen 1955); as a result snags are a preferred foraging substrate for many insectivorous birds (Szaro and Balda 1979). Younger snags contain a larger number of insects (Keen 1955). The degree and type of decay affect the ease with which birds can excavate cavities in snags and how long the snags will stand. As a secondary cavity nester, flammulated owls have a direct relationship with snags; however, the role of snags in flammulated owl foraging ecology has not been explored.

Snag densities in ponderosa pine forests vary; the data of Cunningham *et al.* (1980) suggest that 5.2 snags per ha is an average density for mature ponderosa pine forest. Covington and Moore (1994) estimate that the density of ponderosa pine snags, downed logs, and stumps declined from 5.3 to 1.4 per acre in the last 120 years on an unlogged site in Arizona. Cunningham *et al.* (1980) felt it would be impossible to predict the number of snags standing in pristine old forest. However, promising approaches include simulations (Keane *et al.* 1990), analysis of old photographs (Lehmkuhl *et al.* 1993), and reconstruction of presettlement stand structure based upon tree rings (Covington and Moore 1992, 1994).

Snags are produced when forest fires, insects, diseases, or lightning kill trees. About 30% of standing snags fall within the first 5 to 15 years after the trees die (Keen 1955, Cunningham *et al.* 1980). In California, Keen (1955) found that only 10% of snags were standing after 25 years. In contrast, Cunningham *et al.* (1980) found that 40% of the snags were standing after 25 years and 25% were still standing after 50 years in Arizona. The sites studied in Arizona are drier than in California, which might limit rates of decay (Cunningham *et al.* 1980).

A major question concerns how much downed and dead woody debris was present in presettlement forests, but it was probably less on frequently burned sites than is called for in many old-growth criteria. Downed logs and branches greater than 8 cm in diameter provide crucial ecological functions, including shading microsites for conifer regeneration, serving as sites of mycorrhizal activity and sediment traps, and affecting soil erosion, energy flow, and nutrient cycling (Harvey *et al.* 1987, 1988). The downed woody material is used by more than 175 species of small mammals and birds (Maser *et al.* 1979). Decaying logs provide refuge for fungi during and immediately following disturbance (Harvey *et al.* 1979, 1988). They are often dense with roots, fungal hyphae, nitrogen-fixing bacteria, and other organisms (Harvey *et al.* 1979, 1988). The ecological role of woody debris varies with climate, biomass, size, arrangement, decay, and forest structure (Kaufmann 1990). Woody debris has accumulated since the advent of fire exclusion, even where stands have been harvested (Parsons and DeBenedetti 1979, Barrett 1988).

SUCCESSION AND DISTURBANCE

Fire is the most common natural disturbance and one of the most important ecosystem processes in

ponderosa and Jeffrey pine forests. Disturbance by fire, insects, disease, lightning, and wind are inevitable in ponderosa pine forests. The healthy functioning of ecosystems is dependent on periodic tree mortality that recycles nutrients, enhances decomposition, favors regeneration, and maintains photosynthesis and production. In addition, as decaying wood is incorporated into the soil, it enhances nutrient cycling, water retention, and mycorrhizal populations; many roots are found in the organic layers in the soil (Harvey *et al.* 1979, 1987, 1988).

Excluding disturbance from pine forests is not only impossible, but it has undesirable ecological consequences. Insects and diseases are essential components of ecosystems, for they are regulators of ecosystem productivity and stability (Perry 1988, Schowalter 1988).

Fire as an Ecosystem Process

Fire has played a critical ecological role in ponderosa and Jeffrey pine forest ecosystems. Substantial changes in the temporal and spatial pattern of fires significantly affect the structure, function, and sustainability of these forest ecosystems. Fire plays a direct role in vegetation succession, nutrient cycling, soil structure and stability, and regeneration (Kaufmann 1990). Fire also influences age structure, species composition, and productivity, which in turn influence flammulated owls (Chapter 4). With less frequent fires, entire landscapes have changed, especially where fire exclusion coincided with extensive timber harvest and grazing (table 1).

Although fires are often suppressed, low-intensity surface fires benefit ponderosa pine forests. In the absence of fire, open stands of ponderosa pine have been replaced by dense stands that may have reduced value for flammulated owls. On many sites, less frequent fires have promoted succession to less fire-resistant and often more flammable tree species. Such stands are commonly less productive for quality timber and forage, more susceptible to disease and insect problems, less aesthetically pleasing, and more prone to damaging crown fires. Forest health is declining dramatically in some regions such as the Blue Mountains of Oregon (Mutch *et al.* 1993). Epidemic insect infestations and large catastrophic wildfires have increased tree mortality, causing undesirable ecosystem changes. Weaver (1974) voiced concerns about the effects of fire suppression:

The great increase in fire hazard is the most ominous change since earlier days. The very success of foresters in suppressing fires has radically changed conditions described by Muir and other

Table 1.—Forest ecosystems change when fires are less frequent (Arno 1976, 1988, Barrett 1988, Cooper 1960, Covington and Moore 1992, 1994, Covington and Sackett 1984, 1986, 1990, Keane *et al.* 1990, Laudenslayer *et al.* 1989, Lotan and Morgan 1993, White 1986, Steele *et al.* 1986, Weaver 1974).

When fires are less frequent:

- Tree density increases, especially small-diameter tree
 - Species composition changes
 - More shade-tolerant trees establish
 - Shrub and herbaceous vegetation is less diverse
 - Understory vegetation is less productive
 - Fuels accumulate on the forest floor (duff, litter, woody debris) and in the crowns of trees
 - Organic matter decomposition slows
 - Nitrogen mineralization declines
 - Nutrient cycles stagnate
 - Crown fires are more likely
 - Crown fuel loading increases
 - Fuels are more continuous horizontally
 - Fuels are more continuous vertically
 - Fire size and intensity increases
 - Trees are less vigorous
 - Tree mortality due to insects and disease increases
 - Patterns and processes are simplified at many spatial scales
 - Stands are less aesthetically pleasing
 - Landscapes are more homogeneous
 - Canopy closure is greater
-

early observers. Great advances have been made in fire prevention and suppression, and fewer fires escape control. When they do, however, and they still do and will continue to, they usually are devastating. Uninterrupted fuel accumulations in the past 40-50 years together with the development of reproduction and brush thickets have made it extremely difficult to control such fires, and the costs of control may properly be described as fantastic [p. 300].

Fuels accumulate in the absence of fire. Much of the fuel loading in ponderosa pine stands consists of forest floor material (litter, duff, and small-diameter woody debris). The amount of forest floor material can affect production and composition of understory vegetation (Pase 1958), soil temperature and moisture regimes, tree germination and survival (Pearson 1950), soil nutrient availability (Moir 1966), and erosion (Johnson 1940). Fuel loading in ponderosa pine forests is extremely variable (Sackett 1979).

As litter accumulates in the absence of fire, rates of organic matter decomposition and nitrogen mineralization decrease (White 1986). Although some nitrogen is volatilized and lost during fire, such loss is limited, and nitrogen availability often increases through nitrogen fixation if fires are not severe. Covington and Sackett (1984) and Ryan and Covington (1986) found increased availability of nitrogen, phosphorous, potassium, calcium, and mag-

nesium in the first year following a prescribed burn. Four years after burning, nutrient content of soils and foliage were the same in burned and unburned stands (Covington and Sackett 1984, Landsberg *et al.* 1984). In Arizona, repeated burning at intervals approximating the presettlement fire-free interval increased extractable nitrogen, suggesting that low-intensity fires enhance nutrient cycling (Covington and Sackett 1986). Fire exclusion and the selective logging of larger trees increased the intensity and duration of epidemics of root diseases, dwarf mistletoes, and insects (Hessburg *et al.* 1993). If current trends continue, not only might high tree mortality during epidemics prevent development of late successional forests, but they may also increasingly threaten remnant old forests (Covington *et al.* in press).

Fire Effects

Fire exclusion has contributed to dramatic changes in ponderosa pine forest structure. Fire is an important ecological process in the Southwest (Covington and Moore 1994), Utah (Madany and West 1983) Montana (Gruell *et al.* 1982, Keane *et al.* 1990), Idaho (Steele *et al.* 1986, Barrett 1988), Oregon and Washington (Weaver 1959, Lehmkuhl *et al.* 1993, Everett *et al.* 1994), and California (van Wagtendonk 1985, Laudenslayer *et al.* 1989).

Ponderosa and Jeffrey pine are more resistant to

damage from surface fires than any associated tree species except western larch (Flint 1925). Both are very resistant to scorch, for their high, open crowns, large buds, and high foliar moisture content limit desiccation from the heated air above the flames. Both also have thick bark that insulates the cambium on large trees. Seedlings are often killed by fires, and even large trees are easily killed by fires that burn through the crowns of the trees. Trees are more likely to die when fuels have accumulated through timber harvest or fire exclusion, where stands are dense (more than 100 trees per hectare), or where ladder fuels form as shrubs and small trees that can carry flames into the crowns of the large trees (Kilgore and Curtis 1987).

If trees are weakened and stressed by excessive scorch or cambial damage, bark beetles or diseases often kill them (Harrington 1987). The percentage of the crown that is scorched is a good predictor of mortality in ponderosa pine (Saveland and Neuenschwander 1989), and mortality is low until more than 90% of the crown is scorched (Wyant *et al.* 1986, Harrington 1987, Saveland and Neuenschwander 1989). Cambial damage seldom kills trees unless there is damage in all four quadrants of a stem section.

Cooper (1960), White (1985), Habeck (1990) and Arno and Scott (1993) described stands that developed through episodic regeneration. Regeneration follows death of overstory trees killed by lightning, insects, disease, windthrow, or fire. Establishment is episodic, relying on a combination of conditions that allows for seedbed preparation (usually by fire), reduction of competition, sufficient seed, climatic conditions suitable for germination and survival of seedlings, and fuel and fire conditions conducive to seedling survival. Such events are seldom synchronous. Irregular fire intervals play an important role in regeneration where fires are very frequent. Longer intervals between individual fires would allow ponderosa pine to achieve sufficient size to survive subsequent fires while also permitting encroachment of more shade-tolerant and less fire-tolerant tree species (Keane *et al.* 1990).

Fires often alter the composition and productivity of the vegetation. The ecological role of fire in ponderosa pine forests, particularly as fire affects species composition, has been summarized in general by Wright (1978) and by habitat type groups by Davis *et al.* (1980), Fischer and Clayton (1983), Crane and Fischer (1986), and Fischer and Bradley (1987).

Most of the shrub species common in ponderosa pine forests recover very rapidly following fire; many are favored by frequent fires. Very frequent (1

to 5 years between burns) fires favor herbaceous vegetation over shrubs. Most understory species are dependent on recurrent fire or other disturbance to maintain productivity. Many species resprout or establish quickly from buried seed. Overstory density, which often increases in the absence of fire, has a major impact on understory productivity. Wright (1978) provided an excellent overview of the ecological effects of fire in ponderosa pine forests. Another good source of such information is the Fire Effects Information System, a computerized synthesis of literature (McMurray 1988).

Prescribed fire is useful for managing structure and composition of vegetation, enhancing nutrient cycling, and reducing the probability of destructive fires. Using frequent prescribed fires can be an integral part of enhancing and maintaining the health of ponderosa and Jeffrey pine ecosystems (Mutch *et al.* 1993). Moir and Dieterich (1988) highlight the importance of fire to direct succession toward an old forest condition. They feel that recurrent fires are needed both to maintain quality old forest and to lessen the probability of stand-replacing fire events. They are very concerned that management over the last 100 years has jeopardized the ecological conditions and values of old forest. Dwarf mistletoe is now a major cause of mortality in large ponderosa pine, which may predispose these trees to bark beetle attack.

Martin *et al.* (1989) recently reviewed the use of prescribed fire to reduce wildfire hazard. Weaver (1955) found an 82% reduction in number, a 65% reduction in average size, and a 94% reduction of the total area burned in the 3 fire seasons following prescribed burning of 26,000 hectares on the Fort Apache Indian Reservation in Arizona. In Washington, Weaver (1957) similarly found that 90% fewer hectares burned, and damage and costs were reduced by 94% and 79%, respectively, following prescribed burns. Fuels do accumulate following fire, particularly if foliage or trees die, so frequent fires may be required to maintain low fire hazards. Guidelines for prescribed burning in ponderosa pine forests have been written for the Southwest (Harrington 1981) and Intermountain West (Kilgore and Curtis 1987).

Timber Harvest

Ponderosa pine forests can be successfully managed for timber production under a variety of even- and uneven-aged systems. Where ponderosa and Jeffrey pine are managed intensively, even-aged harvest and regeneration systems are used most often.

See Smith (1986) for a general discussion of the practice of silviculture. Barrett (1980), Burns (1983), and Lotan and Morgan (1993) provide descriptions of silvicultural systems applied in ponderosa and Jeffrey pine forests and how these vary geographically.

Even-aged systems such as clearcut, seed tree, and shelterwood are designed to regenerate all trees at about the same time. In clearcuts, all trees are harvested at once in blocks, strips, or patches that are usually 4-40 ha in size (sometimes much larger) depending on species ecology, administrative constraints, and economic considerations. With the seed tree and shelterwood systems, large residual trees are left to provide seed. In shelterwood cuts, the residual trees also provide shade and wind protection for the young tree seedlings. The overstory trees are usually removed as soon as regenerating trees are established. In any of these systems, large trees can be retained for all or part of the rotation. Such retention adds vertical structure to the managed stands, provides seed to regenerate small gaps, and through time contributes to soil development once the trees die and fall to the ground.

Uneven-aged silvicultural systems are used to create and manage forests with 3 or more age classes. Single trees or small groups are removed in periodic harvests. Sometimes resembling small clearcuts, such systems rely primarily upon natural regeneration. In theory, trees of all ages and diameters are harvested at each entry, including the younger and smaller trees in the stand. However, in practice this is not always done. Selection cuts are designed to mimic gap-replacement forest succession and thus create small-scale diversity.

Regeneration can be obtained naturally or artificially. On a Douglas-fir habitat type in central Idaho, natural regeneration was most successful within group selection, seed tree, or 0.4 to 0.6 ha clearcuts, and most seedlings were found within 30 m of the seed source (Steele *et al.* 1989). In addition, up to 20% of the ponderosa pine seedlings established from seed cached by animals or birds. In contrast, ponderosa pine did not always readily establish following logging or burning on a grand fir habitat type (Steele *et al.* 1987).

Often, harvests in ponderosa and Jeffrey pine forests is opportunistic and does not follow a particular silvicultural system. While this was more true in the past, many trees are cut to meet short-term objectives without long-term site productivity in mind.

Harvesting usually simplifies forest structure at spatial scales from individual trees to stands and forest watersheds. However, harvesting can be designed to enhance structural diversity at any of these

scales through retention of residual trees, variation in patch size, use of some very long rotations, and sensitivity to existing structural diversity. Prescriptions should consider landscape-level issues such as the connectivity between patches of different types and the risks (e.g., fire spread) and benefits (e.g., species dispersal and habitat quality) of juxtaposition in spatial patterns at multiple scales.

Although snags can pose fire and safety hazards and be the target of firewood cutters, silvicultural treatments can readily be designed to create and provide the snag density and quality needed for particular wildlife species. Thus, green trees can be retained and/or girdled, and dead or dying trees can be left standing to create snags with the diameter, height, and degree of decay needed by particular cavity-nesting birds (Thomas *et al.* 1979a) or to provide woody debris to soil to maintain long-term site productivity.

Insects

Insects are most abundant in early successional stages and in old forest, both conditions where forest structures are diverse and there are abundant grasses and shrubs. Furniss and Carolin (1977) state that there are up to four times as many lepidopterans associated with ponderosa pine and Douglas-fir forests as other forest types. Most of the information on insects in ponderosa pine forests applies to those insects that feed on trees. As many as 198 different insect species feed on ponderosa and Jeffrey pine foliage, seed, phloem, and other tissues (Furniss and Carolin 1977, Schmid 1988, Jenkinson 1990, Oliver and Ryker 1990).

Bark beetles, including mountain pine beetle (*Dendroctonus ponderosae*), western pine beetle (*D. brevicornis*), *D. jeffreyi*, and other *Dendroctonus* and *Ips* species, are the most likely insects to kill ponderosa and Jeffrey pine trees. Trees die through a combination of blue stain fungus transmitted by the beetle and from phloem consumption by bark beetle larvae. At endemic levels, old and less vigorous trees die, usually in patches. However, when bark beetle outbreaks occur, even young, small-diameter trees die. Tree vigor affects the ability of the tree to survive; it is the larger trees with thick phloem and declining growth rates that are most susceptible. Trees in dense stands supporting basal areas over 34 m² per hectare are more likely to be attacked; thinning to maintain vigor of individual trees is effective (Sartwell and Stevens 1975). Bark beetles typically attack trees that are weakened by disease, competition, defoliation, injury, or drought.

Mountain pine beetle epidemics develop over several years (Sartwell 1971). At endemic levels, fewer than 12 trees/ha are killed each year either as widely scattered single trees or in groups of 2 to 3. During the first year of an epidemic, 12 to 30 trees/ha are killed, sometimes in groups of 3 to 5. Two to four years later, 75 to 370 trees/ha may die each year. Bark beetle populations usually decline naturally within 6 to 8 years. Outbreaks are shorter on good sites than on poor ones (Sartwell 1971). There is some evidence that predation by insectivorous birds affects bark beetle populations, particularly at endemic levels (Thomas 1979). For this reason and because susceptible trees are more scattered in spatially diverse stands (Perry 1988), patchy forests with mixed age and species composition are less prone to bark beetle outbreaks. Once predicted to decline in abundance after virgin timber was cut, bark beetles currently kill many trees in dense, even-aged stands over large areas (Sartwell 1971).

Dwarf Mistletoe and Other Pathogens

Dwarf mistletoes cause the most common disease in ponderosa and Jeffrey pine. *Arceuthobium campylopodum* infects both ponderosa pine and Jeffrey pine in California and the Northwest. In the southwestern United States, *A. vaginatum* infects trees on one-third of the commercial forest (Oliver and Ryker 1990), slowing tree growth and killing ponderosa pine. Mortality rates due to dwarf mistletoe are higher in the Southwest than in other parts of the range; dwarf mistletoe is absent from the Black Hills of South Dakota (Hawksworth and Shaw 1988). Alexander (1986) considered dwarf mistletoe one of the most serious diseases of ponderosa pine.

Dwarf mistletoes are parasitic flowering plants. Plants establish from seed and grow on branches and stems of trees. Infected branches often swell and witches' brooms may develop. Although dwarf mistletoes are more common on poorer sites, the greatest development is on fast-growing, vigorous trees. The parasite spreads by seed, so lower branches and adjacent trees are more affected. The infection often spreads from taller to shorter trees. Dwarf mistletoes alter the structure of a forest by reducing growth and increasing tree mortality. Mortality during drought is more severe. Severely infected stands of ponderosa pine can become stagnated, or, if mortality is high, may revert to a grass, forb, and/or shrub stage. Severe infestations result when the parasite continually intensifies over long periods of time. Infected trees are less vigorous and often susceptible to bark beetles or other diseases.

Fire was the primary natural control for dwarf mistletoe. Prescribed fire can be used to reduce the severity of dwarf mistletoe infection (Harrington and Hawksworth 1992). Infected trees tend to have lower crowns, more of the highly flammable witches' brooms and a fire-induced mortality rate twice that of uninfected trees (Harrington and Hawksworth 1992).

Root diseases include annosus (*Heterobasidium annosum*), armillaria (*Armillaria* spp.), and black stain (*Leptographium* [syn. *Verticicladiella*] *wagneri*). Root rot kills trees in patches; root-rot infection centers spread outward at up to 1 m per year (Oliver and Ryker 1990). Active infection centers can result in windthrow as roots are weakened. Ponderosa pine is resistant to root diseases compared to other conifers with which it is found (Oliver and Ryker 1990).

Heart rot is caused by fungi. Trees infected with heart rots have softer wood, which facilitates excavation by woodpeckers (Gilbertson 1980). Ponderosa pines infected with heart rot produce snags preferred for nesting by woodpeckers in Montana (McClelland 1977).

Other Disturbance

Lightning ignites fires and strikes trees, often damaging but seldom killing trees. Mortality is rare unless trees are more than 175 years old (Pearson 1950); mature and decadent trees are more often killed. Mature and decadent trees are more likely to fall in the wind, but the well-developed root system limits windthrow.

Ponderosa pine is sensitive to air pollution (see review in Lotan and Morgan 1993). Ozone (Miller *et al.* 1963) and acid rain (McColl and Johnson 1983) and other airborne pollutants cause physiological damage, decline in vigor, and eventual mortality. Stressed trees are also more susceptible to insect and disease mortality. Air pollution presumably caused the common chlorosis and related forest decline in Jeffrey pine in the Sierra Nevada and San Bernadino mountains in California (Barbour 1988).

SUCCESSIONAL PATTERNS

Successional patterns have been described for ponderosa pine forests in Montana (Fischer and Clayton 1983, Fischer and Bradley 1987), in Utah (Bradley *et al.* 1992), in Idaho (Steele *et al.* 1987, 1989), and in Arizona and New Mexico (Moir and Dieterich 1988). The successional patterns described here are drawn from these sources. This description emphasizes the successional patterns where fire is the primary dis-

turbance. Later discussion includes the effects of logging and grazing. This discussion of successional patterns applies to individual patches within stands.

Recurrent low-intensity fires created and maintained old forest on dry, warm sites where perennial grasses dominated the understory vegetation (figure 4) (letters in subsequent paragraphs refer to figure). Any fire burning in open, park-like ponderosa pine stands (A) will create the mineral soil seedbed for trees to regenerate. Open stands will be maintained if subsequent fires occur soon enough to kill all or most of the seedlings. In the absence of fire for long intervals, tree seedlings grow to sufficient size to survive subsequent fires. If the grasses and shrubs are not very vigorous, pine seeds are abundant, and weather is favorable, many seedlings will establish at once (B2); if not, the younger trees will be uneven-aged (B1). When the surviving seedlings are of similar age, with time, the stands become dense and crowded and of low productivity (D1 and D2). If low intensity fires occur, they thin these stands, but severe stand-replacing fires become increasingly likely. Severe fires replace the stand, as all the trees within a patch or within the entire stand are killed, resulting in a grass or shrub-dominated community (F). This is the most likely scenario where fires have been excluded (Moir and Dieterich 1988). Open, park-like stands can develop if fires of low to moderate intensity thin seedlings (C3). Open stands of pole-sized (D3) and larger (E3) trees are the most likely candidates for developing into old forest stands (Moir and Dieterich 1988). Stand development depends on the establishment, growth, and death of individual trees (White 1985).

Succession from a grass community (F) depends on whether many seedlings establish at once and whether fires occur before many of the seedlings are large enough to survive burning. Dense, closed-canopy stands can result (H1, I1, H2, I2). Such stands develop where fires have been excluded for 30 years or more (Moir and Dieterich 1988). Again, if fires are infrequent, stand-replacing fires become more and more likely, which results in a return to the grass stage (F). If low to moderate intensity fires occur in the pole stands (within 10 to 15 years in Arizona, Moir and Dieterich 1988), open, parklike stands of progressively larger-diameter yellow pine trees (I3, J3, A) may result through recurrent fires and advancing succession. The old forests (A) consist of large trees (often greater than 50 cm dbh and 150 years or more old) with snags and occasional downed logs (Moir and Dieterich 1988). If fires do not occur often, the old forest may degenerate when thickets of young trees establish under an open stand of large

diameter trees and snags (Moir and Dieterich 1988). Clearly, it is difficult to develop the diverse structure of old ponderosa pine forests without recurrent fire, particularly on sites where ponderosa pine is seral. Moir and Dieterich (1988) suggest that open, 150- to 200-year old stands (I3) are the best candidates for developing the diverse structure and unique functional attributes of old forests.

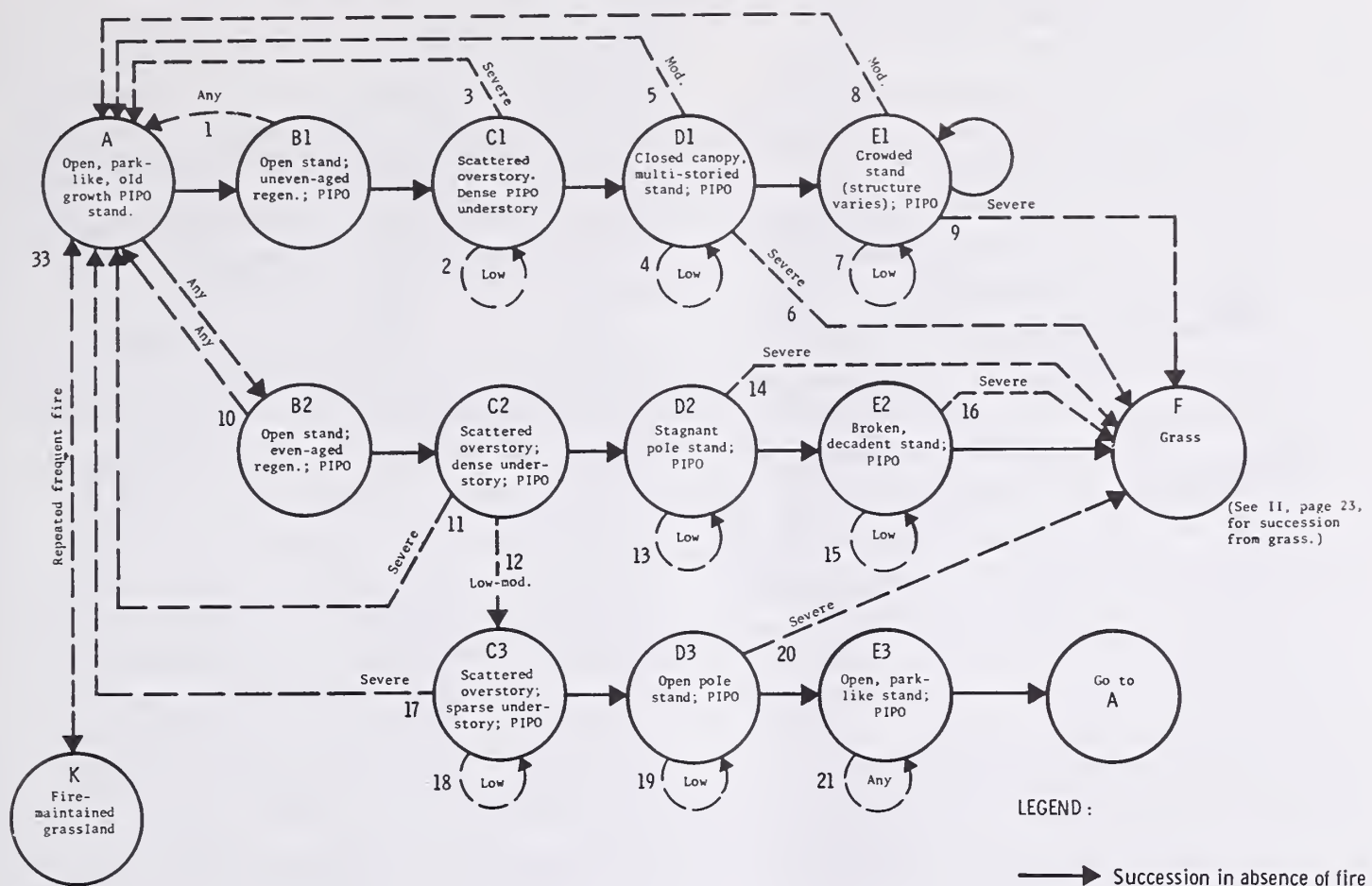
On more mesic sites the patterns of succession are similar (figure 5), but the forests tend to be more dense, regeneration is more often even-aged, and shrubs are a more common part of the understory (Fischer and Clayton 1983). "Doghair" thickets of small-diameter trees are also more common. The doghair thickets don't readily burn, but when they do, stand-replacing fires often result. In the absence of thinning by fire or cutting, these stands stagnate for many years. On still more mesic sites where grand fir is the climax tree species, open, park-like stands of ponderosa pine, western larch, and other tree species occur, but only if fires are frequent enough to limit encroachment by the more shade-tolerant and less fire-resistant fir.

Successional patterns differ depending on the associated tree, shrub, and grass species. For instance, gambel oak (*Quercus gambellii*) and aspen (*Populus tremuloides*) resprout vigorously following fire; both dominate following stand-replacing fires. These and other shrubs may present significant competition that limits the number and growth of young ponderosa pine seedlings (Steele *et al.* 1987, 1989; Bradley *et al.* 1992). Unfortunately, successional patterns are not described for most ponderosa pine forests. Steele *et al.* (1987, 1989) include a wealth of information about the succession within the tree, shrub, and forb layers on two habitat types in central Idaho.

Grasses and shrubs are most productive when tree canopy density is low. As a result, the open stands are very important to insect production, which explains the observation of many bird species feeding in these stages (Thomas *et al.* 1979b). The goals of intensive management for timber production are to shorten early succession and eliminate the latest stages.

Recurrent, low-intensity fires result in the presettlement pattern of succession leading to open, parklike, uneven-aged pine stands in which stand-replacing fires are very unlikely. Succession in the absence of fire will most likely result in a snag forest with a grass or shrub understory when a high-intensity stand-replacing fire inevitably results (Moir and Dieterich 1988, Covington and Moore 1994). As fire frequency has declined, not only remnant old forests, but stands in many other stages of succession are also at risk from stand-replacing fires

I. SUCCESSION FROM THE OPEN, PARKLIKE, OLD GROWTH PONDEROSA PINE STATE



LEGEND:

- Succession in absence of fire
- - - - - Response to fire
- Low Cool or light surface fire
- Mod. Fire of intermediate (moderate) severity
- Severe Hot, stand-destroying fire
- 1, 2, etc. Reference number, (see text)

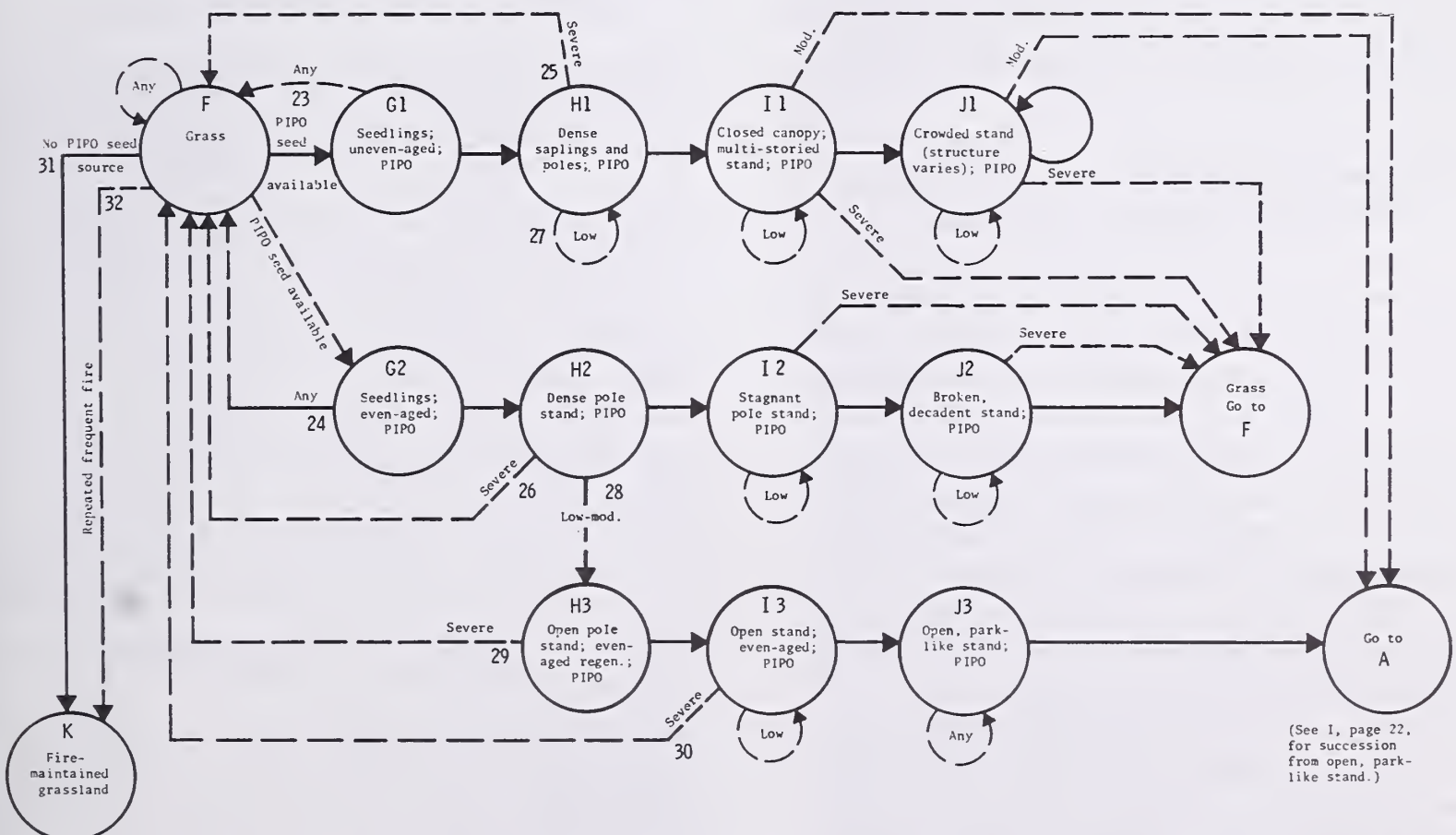


Figure 4.--Hypothesized successional pathways in dry, warm ponderosa pine forests in Montana, Arizona, and New Mexico. Such sites include habitat types where ponderosa pine is the sole climax dominant tree growing with perennial bunchgrasses such as wheatgrasses (*Agropyron* spp.), fescue (*Festuca* spp.), or low shrubs such as bitterbrush (*Purshia tridentata*) or snowberry (*Symphoricarpos albus* or *S. occidentalis*). Adapted from Fischer and Clayton (1983).

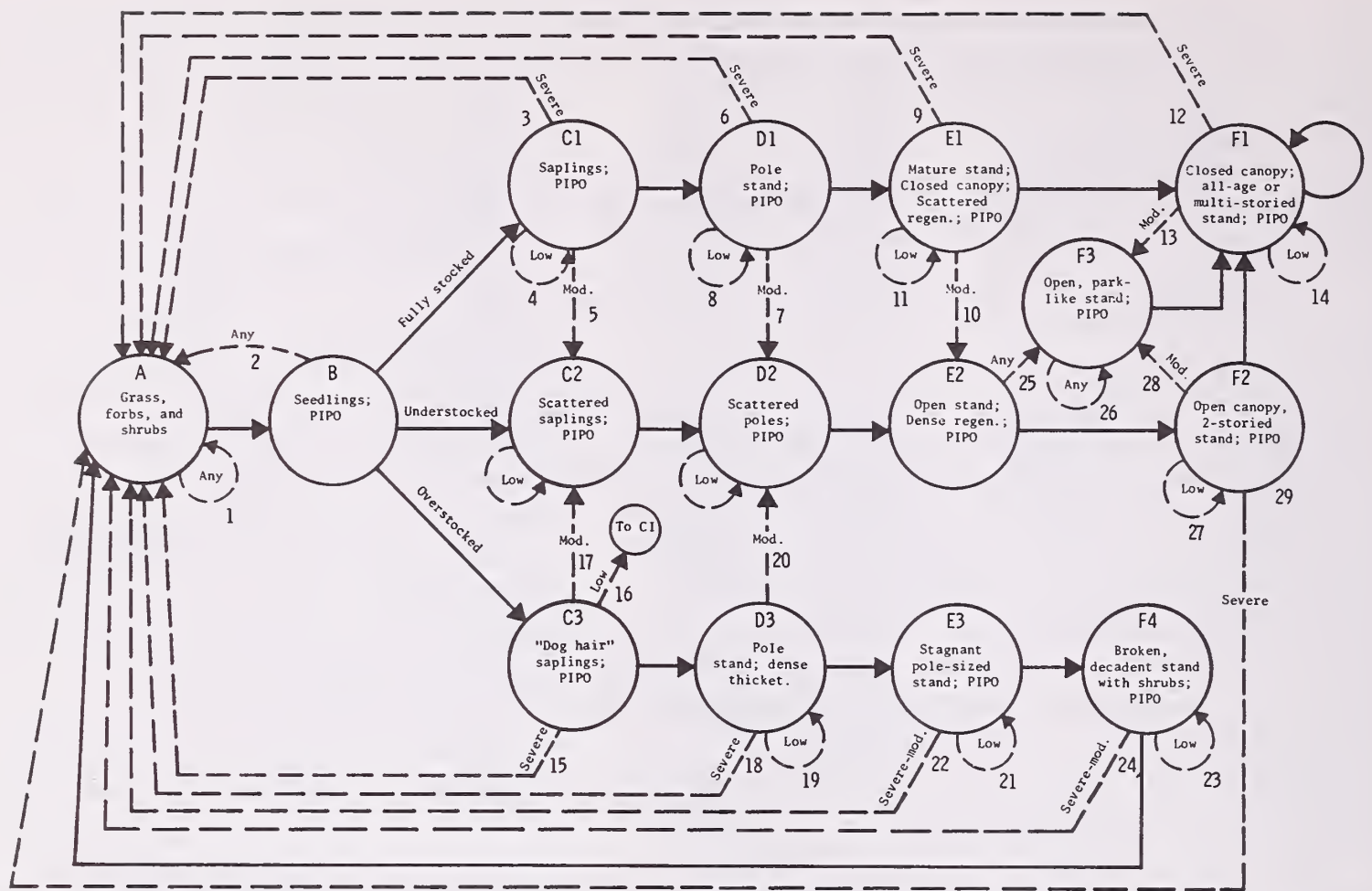


Figure 5.--Hypothesized successional pathways in warm, moist ponderosa pine forests in Montana. Such sites include habitat types where ponderosa pine grows with snowberry (*Symphoricarpos albus*), chokecherry (*Prunus virginiana*), and buffaloberry (*Shepherdia canadensis*). Adapted from Fischer and Clayton (1983).

(Lehmkuhl *et al.* 1993). Arno (1988) and Moir and Dieterich (1988) feel that prescribed fire could be used very effectively to alter successional pathways to encourage development of the unique structure of old forests.

Contrasting Patterns of Succession Following Logging and Fire

The frequency of forest disturbance from timber harvesting varies with the management objectives, the silvicultural system applied, and the site productivity. It is difficult to generalize about differences in succession following logging and fire because both are variable in severity. Also, fire is frequently used following harvest operations. As with fire, the more severe logging disturbances are less frequent. In the absence of harvest, trees are killed by diseases, insects, fire, and windthrow, in order of decreasing importance (Schubert 1974).

Harvesting operations and fires that are most severe remove most of the tree canopy volume, expose and displace much mineral soil, and remove or displace most organic material on the soil surface. Less severe harvest and fire result in minimal disturbance of understory vegetation.

Logging and fire have variable but significantly

different effects on soils and organic matter. Unfortunately, soil ecosystem structure and function are not well understood, despite the fact that soil processes determine many aboveground structures and functions. Soil organic matter is very important to the long-term productivity of forest soils (Harvey *et al.* 1979, 1987). Because soils are fundamental to biogeochemical cycling, alteration of the physical and chemical properties of soils may affect whole forest ecosystems. Where organic matter has been removed completely or displaced during disturbance, growth may be slowed and the overall productivity of the site reduced. Short, ectomycorrhizal roots of seedlings and old trees are concentrated in or just below soil organic layers (Harvey *et al.* 1988). Surface organic layers also protect the soil and root systems from compaction that occurs when heavy machinery is driven over soil (Gracean and Sands 1980). Erosion can increase dramatically under poor management, particularly on steep slopes with unstable soils and where there is little duff or vegetative cover to protect soils (Gary 1975). Water quality declines if disturbance of the surface soils is excessive or if the trees shading streams and filtering sediments are removed. If soils are disturbed and the cover of forest litter is reduced through road construction, harvesting, and / or severe fires, infiltration will decline

and increased erosion may result.

Timber harvest and prescribed fire increases understory forage production (Ryker and Losensky 1983). Herbaceous production increased following fires that killed some trees and consumed duff and litter, thus creating a more open forest with increased rates of decomposition of the forest floor (Oswald and Covington 1984); nutrient values also increased (Harris and Covington 1983, Andariese and Covington 1986).

One of the major differences between logging and fires is the abundance of residual snags and woody debris. Stand-replacing fires differ from clearcuts because, although trees are killed by fires, the trees become snags and eventually woody debris incorporated into the forest soil. In addition, timber harvest tends to simplify the horizontal and vertical structure of forest ecosystems. Fires leave more diverse patterns and composition, particularly if the fires are not stand-replacing over large areas.

Arno (1988) recommends managing both climax and seral ponderosa pine stands with a combination of cutting techniques, such as thinning and improvement cuts, in combination with regular prescribed burning. He believes this would promote development of productive stands, favor regeneration, and reduce the risk of damage in severe wildfires.

FUTURE VEGETATION PATTERNS

Where fire frequency has declined, we now often find thickets of small suppressed grand fir and Douglas-fir trees being severely defoliated by western spruce budworm; killed by bark beetles, root diseases, and dwarf mistletoe; and threatened by wildfires (Hessburg *et al.* 1993, Mutch *et al.* 1993). Such forests are not sustainable (Hessburg *et al.* 1993, Everett *et al.* 1994). They provide reduced habitat for many wildlife species (Covington and Moore 1994), and provide few of the values people draw from ponderosa pine forests (Covington and Moore 1994). Even remnants of old forests that are veterans of repeated disturbance are at greater risk when they are surrounded by dense continuous forests.

Ecological Restoration

Covington and Moore (1994) feel that if we are to restore forest structure to conserve biological diversity, we must do so within the next 15-30 years. After that, crown fire, insects, and diseases will kill many of the trees of presettlement origin (Covington and Moore 1994). Restoration of this type may have

important implications for flammulated owls.

Fire will be useful in ecological restoration. Fire can be used to maintain open, parklike stands of ponderosa pine and dominance by ponderosa pine in mixed stands. This has been shown in simulations of the effects of different fire regimes (van Wagendonk 1985, Keane *et al.* 1990) and results of prescribed fires conducted at regular and varying intervals (Harrington and Sackett 1992). Prescribed burns will be required in addition to natural lightning fires if the goal is to mimic the effect of presettlement disturbance regimes on ecosystems, particularly where stands have now become isolated enough to prevent fire spread from adjacent areas. Reintroduction of prescribed fire into stands where fires have been suppressed for a long time will, however, require great care. Unless the accumulated down and dead woody debris, duff, and litter and dense patches are reduced gradually in successive fires or are physically removed prior to burning, even large trees with thick bark may suffer high mortality in low-intensity fires (Sackett 1980, Harrington and Sackett 1992). Restoring the ecosystems using fire will often require initial mechanical treatments. Experiments to combine prescribed fire with removal of small-diameter trees and fuels on the forest floor are underway in Arizona (Covington and Moore 1994) and elsewhere.

In old-forest stands in Arizona, where fires had been suppressed for more than 100 years, large-diameter pines with thick bark and high open crowns died following prescribed burning (Harrington and Sackett 1992). Mortality was caused by root damage induced through soil heating due to slow burning of very heavy duff and litter accumulations. Raking heavy duff and litter accumulations from around the base of these large trees will improve survival in the first burns that follow long periods of fire exclusion. Successive burns can also be used to reduce fuels to acceptable levels without site damage (Weaver 1957, Biswell 1963).

Restoring the health of many ponderosa pine forests will require large-scale use of prescribed fire with judicious partial cutting to maintain much lower tree densities and a more open coniferous forest understory than now exists in ponderosa pine and western larch stands (Mutch *et al.* 1993). Mutch *et al.* (1993) recommend a 10-fold increase in the use of prescribed burning to restore the health of ponderosa pine and mixed-conifer forests in the Blue Mountains of Oregon. To do so will require new and sometimes dramatically different financing, planning, and conducting prescribed fires (Mutch *et al.* 1993). Fires, whether prescribed or wildfires, pro-

duce smoke that can impair visibility, air quality, and human health. Thus, increased use of prescribed fire will have to be based on careful analysis and public understanding of the tradeoffs among "increased prescribed fire, inevitable wildfire, ecosystem health, and public exposure to smoke" (Mutch *et al.* 1993).

Changing Environments

Climates could change significantly over the next 100 years if the equilibrium temperature of the earth increases by 3 to 5 degrees C as has been projected in global circulation models (Joyce *et al.* 1990). The models all differ in projections for temperature and precipitation changes in specific areas, but rapid change is inevitable and will affect community composition, species fitness, and ecosystem functions. Increasing CO₂ concentration (to double by the middle of the next century) (Shands and Hoffman 1987), increased temperatures, and changed amount and seasonal pattern of precipitation will affect growth and survival of individual organisms, thus altering the species composition and structure of plant communities (Ryan 1991).

Changing climate will directly affect regeneration, photosynthesis, nutrient cycling, decomposition, and other ecosystem processes (see review by Ryan 1991). High temperatures, drought, and nutrient deficiencies lead to stress-induced mortality (Waring 1987). Tree mortality due to insects, diseases, and fires will be the earliest visible effect of global climate change (Joyce *et al.* 1990). More importantly, climate affects fire regimes (Swetnam and Betancourt 1990) that will magnify the effects of climate on ecosystem processes and influence species migration (Ryan 1991). Swetnam and Betancourt (1990) demonstrated the synchrony of large fires throughout the Southwest and low spring precipitation, reduced tree growth, and climate in the tropical Pacific (El-Niño). Below-ground processes may ameliorate or exacerbate vegetation responses to climate change (Klopatek *et al.* 1992).

We cannot currently predict the consequences of changes with certainty. Leverenz and Lev (1987) projected changes in the range of ponderosa pine under several scenarios of climate change. Climate changes will have the most dramatic effects on the extreme sites within the range of a species, i.e., the sites where ponderosa and Jeffrey pine are climax. The overall temperature changes are similar to those experienced during the last 12,000 years (see Paleocology section), but they will be more rapid. With their heavy seeds, infrequent seed crops, and low dispersal rates, ponderosa and Jeffrey pine could

find it very difficult to keep up with changing distributions of suitable habitat. Old forests, which include trees that regenerated in an earlier climate, could be vulnerable, particularly if fuel and structure are such that they are already at risk for stand-replacing fires. Unfortunately, we don't understand how ecosystems will respond to climate change (Ryan 1991), so it is difficult to project how individual species and the communities in which they exist will change in response to the combined and synergistic changes in temperature, moisture, and CO₂ concentration.

INFORMATION NEEDS

We must seek to fill gaps in our ecological knowledge if we wish to predict the consequences of disturbance, whether human-induced or natural. Little attention has been focused upon below-ground processes, yet soils support forest ecosystems. We also do not understand landscape-scale interactions between spatial pattern and ecosystem processes. More research has been done on the ecology of trees than other vegetation, and on the ecology of big game than other fauna, including insects. Information on the amount, spatial pattern, and structure of old forest is rare (Everett *et al.* 1994). Even so, we understand far more about structure than we do about the function of ecosystems. We also do not fully understand the interactions among fire, insects, diseases, and their combined influence on ecosystem function. Understanding the natural disturbance regimes with which ecosystems evolved is central to successfully predicting the consequences of management (White 1979, Morgan *et al.* in press). If we could describe them, we could use the natural range of variability in disturbance frequency and the resulting landscape structure as a guide to management decisions (Swanson *et al.* 1993, Morgan *et al.* in press).

Filling these critical gaps in our understanding is challenging. Given the scale and the complexity of the questions involved, simulation models and careful monitoring of ecosystem responses to landscape management are two promising approaches. Models such as FIRESUM (Keane *et al.* 1990) that are based on the ecological processes involved in forest succession will be helpful in furthering understanding of the ecosystem dynamics. Lack of information should not delay adaptive management (Walters 1986). Given the diverse and rapidly changing physical, biological, social, and political environments in which we find ponderosa pine forests, we are compelled to change our management.

Our ecological understanding of the structure and

function of old forests is limited and will depend upon more extensive study of remnant forests and simulation modeling. Although some mature forests could be managed to develop characteristics of old forests, we don't know how much is necessary to increase or maintain the current abundance of old forests (Everett *et al.* 1994). That should not, however, prevent management, including prescribed burning and ecological restoration of old ponderosa and Jeffrey pine forests.

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Conservation Status of Flammulated Owls in the United States

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INTRODUCTION

The status of the flammulated owl will be evaluated in this chapter by asking a series of critical questions about the species and its habitat. Answers to these questions will be used to reach one of the following conclusions: (1) populations in the United States are secure and will likely remain so given current land management practices; (2) populations are in peril (declining or experiencing some demographic trauma) or are likely to be in peril in the future given current land management practices; or (3) we currently have insufficient knowledge to determine the conservation status of the species. The conclusions reached here are necessarily tentative, given the incomplete state of present knowledge.

Are the Distribution and Abundance of the Flammulated Owl Declining in All or a Major Part of Its Range?

Distribution

It appears very likely that the flammulated owl's distribution has not contracted in North America. Data are insufficient to extend this conclusion to smaller parts of its North American range or to its Middle American range.

The breeding season distribution of the flammulated owl in the United States is now well understood (Chapter 3 and Map 1). Although details remain to be worked out in local areas, the range of the species is approximately coextensive with that of western yellow pine (i.e., *Pinus ponderosa* and *P. jeffreyi*), with some extension into contiguous pinyon forests of similar stature and occupancy of other vegetation types at similar elevations where these species are absent. The major exception is that pine forests of eastern Wyoming, the Dakotas, and Nebraska are not known to lie within the range of the owl. Available evidence, all of which is circumstantial, suggests that the North American distribution of the species has not changed since the first specimen was obtained in 1860.

The species was collected extensively if not intensively in the nineteenth century before major logging episodes and the subsequent shift in fire history of western yellow pine forests. The locations of these specimen records are throughout the current range of the species (Chapter 3, Map 1). None are outside the currently recognized distribution. On the basis of these data, it appears unlikely that the range of the species has contracted or expanded significantly during the past century.

The winter range of flammulated owls that breed in the United States and Canada is not known, although it is suspected to be in southern Mexico and northern Central America. Too few winter data are available to evaluate changes in winter distribution of the species. Despite the comforting picture presented above for the North American breeding distribution, North American populations cannot be assumed to be in no danger as long as their winter distribution is unknown.

Heretofore, the Middle American distribution of the species has been poorly documented. Specimen and nonspecimen records collated for this study support the idea put forth by early naturalists that the owl is restricted to mid-elevation temperate pine forests throughout Mexico, and perhaps also in El Salvador and Guatemala (perhaps only in winter). New localities are being documented in Mexico owing to work by resident and visiting ornithologists (Adolfo Navarro S., pers. comm.). Changes in distribution will be difficult to document, except by revisiting old collecting sites.

Abundance

There is no reliable evidence that the flammulated owl has increased in numbers anywhere in its North American range. Owing to rapidly increasing knowledge of its range, one might suggest that the species has increased in numbers. Most authorities have concluded that this is not the case, but that improved detection techniques have led to more frequent encounters between researchers or birdwatchers and the owl. Additionally, increases in the number of

birdwatchers in western states, and the desire of many of them to "add this species to their lists," have led to the discovery of many unknown populations. Finally, surveys for spotted owls have incidentally produced new flammulated owl localities.

Although data for testing the hypothesis of change in abundance do not exist, it might be inferred from the increased number of records in recent decades that well-documented changes in pine forest physiognomy have contributed to a population explosion of flammulated owls. McCallum and Gehlbach (1988) examined this inference and rejected it on the basis of their finding that owls nesting in New Mexico evidently preferred an open canopy and low ground cover in front of their nests. The preferred habitat was more similar to presettlement forests than are the heavily stocked stands of the fire-suppression era. Nevertheless, while open forest is apparently preferred for foraging, dense foliage, or at least mistletoe, is apparently used for roosting. It is still possible that the combination of fire-suppression (resulting in dense and often stagnant stands of regeneration) and selective logging (resulting in open stands) may have created a habitat mosaic in some areas that is able to support flammulated owl reproductive activities in the absence of old forest characteristics. This hypothesis would not be tenable if early loggers, like their mid-century counterparts, had removed standing dead trees. In fact, before the advent of chainsaws they often did not, as the test cuts in many hollow, cavity-bearing trees of that era attest.

Evidence for a decrease in abundance is also scanty. Marshall alone (e.g., 1988) has checked old sites, finding the flammulated owl absent in cut-over forests in California and Veracruz. But timber harvest of the kind practiced early in the 20th century must have made some areas unsuitable for decades. The large hot fires that have resulted from fire suppression efforts must similarly have removed suitable habitat. Fire suppression has also allowed yellow pines to be replaced by other, perhaps less desirable, tree species (Chapter 5). As these formerly open forests have become closed, flammulated owls may well have declined or disappeared from some sites. It therefore seems likely that numbers have decreased in the last century owing to loss of habitat resulting from logging, fire, and stand type conversions. This does not mean that persisting populations are inviable, just that total numbers likely have decreased. Losses of this kind do not seem to have reduced the range of the species. The viability of existing populations remains unverified.

Do Habitats Vary in Their Capacity to Support Flammulated Owl Populations or to Support Particular Functional Activities of the Owl?

What Are the Important Characteristics of the High Quality Habitats?

Habitats do vary in their capacity to support populations and functional activities such as nesting, foraging, and roosting. The flammulated owl, though widespread and locally abundant, is a habitat specialist. Its range and abundance are functions of the range and abundance of its preferred habitat, not its own ecological amplitude or adaptability. Multiscale analysis of habitat use provides preliminary indications of the habitat characteristics that are essential to the species, although these are hypotheses that remain largely untested. Further exploration of habitat requirements is needed.

At the regional scale, the flammulated owl is restricted year-round to semiarid, cool-temperate climates, which suggests thermoregulatory limits on the habitat it can occupy. Afternoon temperatures may exceed 32° C in occupied areas, but sympatric congeneric species are able to thermoregulate effectively in high ambient temperatures as long as relative humidity is low. Presumably the flammulated owl has similar abilities. Nights are invariably cool to cold in the elevational range it occupies, but apparently the temperature causes little thermodynamic stress as long as food is available. The winter range therefore is probably determined more by thermal constraints on prey activity than by the physiological capabilities of the owl.

At the landscape scale, interior and exterior edge seem to be desirable if not necessary. Grasslands may contain a richer food base than forests during late summer, and interior edge facilitates gleaning of insects from foliage. These factors, plus thermoregulatory constraints, may be responsible for this owl's limitation to pine forests, which happen to occupy the preferred climatic zone and have the preferred physiognomy. Evidence that *Pinus* itself may not be required comes from the occupancy of selectively harvested (and hence open) Douglas-fir stands in the arid interior of British Columbia and certain mountain ranges in Nevada where *Pinus* is absent. However, reproductive success has not been assessed in those habitats.

Occupied home ranges tend to be on ridges and south-facing slopes. These aspects are more likely to support an open stand structure than north-facing slopes and draws, thereby permitting more luxuriant growth of grasses and shrubs that harbor more

phytophagous insects than do conifers. Insects also have longer activity periods and hence higher growth rates in these warmer microclimates. Given these characteristics, it seems more likely that the owls would tolerate the higher temperatures of such sites to obtain home ranges with open stand structure than that they prefer the ambient temperatures and intensity of insolation found there.

At the microhabitat scale, occupied home ranges seem to contain specific characteristics related to nesting, foraging, and roosting. Nesting of course requires a cavity. Nest boxes and natural cavities are used but old woodpecker cavities are used in the vast majority of cases. Most of these are made by sapsuckers, flickers, or pileated woodpeckers, so these species, as well as large trees with dead limbs, may be considered a critical resource for the flammulated owl.

The arthropod prey of this species are captured on the ground, in the air, and on foliage. Open habitat with considerable edge may not only maximize prey density but also facilitate the foraging maneuvers used by this owl.

Recent radio-tracking studies have shown that flammulated owls roost in dense foliage, either in very old trees or in dense stands of subdominant vegetation types (e.g., Douglas-fir). Because the owls also roost in thickets of stunted regeneration where fire is excluded, shade and inaccessibility to predators may be the most significant characteristics of roosting habitat. Detailed information on roost sites in the Colorado study is being prepared for publication (R.T. Reynolds, pers. comm.).

It would appear from this synthesis that the minimal habitat requirements of this species are as follows: (1) cool to moderate air temperatures, with the effects of higher temperatures ameliorable where humidity is low; (2) dense foliage or mistletoe for roosting; (3) open space between trees to promote abundance of phytophagous insects and facilitate aerial maneuvering by the owl while capturing insects; (4) cavities large and deep enough to allow nesting; and (5) perhaps other unspecified characteristics of old mid-elevation forests of yellow pine, Douglas-fir, and aspen, such as specific prey taxa.

Do Habitats Vary in Their Capacity to Support Principal Prey Species?

Habitats vary in their capacity to support prey, but whether this controls distribution is unclear. The diet of the flammulated owl appears to vary with availability of a broad range of arthropods. The only apparently essential prey are noctuids, which are large,

cold-hardy nocturnal moths that are abundant in spring and summer when other arthropods are not active or abundant. Whether these are equally abundant in Douglas-fir and yellow pine forests is not known. Otherwise, the relevant source of variation among habitats appears to lie in the abundance and diversity of the arthropods they support, rather than the particular kinds. Because open forests support more shrub and herb growth than closed-canopy forests, the greater foliage volume may support more insects. This is consistent with the low insect abundance in conifer forests when compared to broad-leaved forests and suggests that flammulated owls may nest in broad-leaved forests if other requisites are available. This is apparently the case in aspen forests in Colorado and Nevada.

The presence of grasshoppers in the diets of flammulated owls in numerous localities suggests that proximity to savanna grasslands is a positive habitat attribute. A significant proportion of large patches of grassland will not be accessible to the owls. Consistently high reproductive success in a study site lacking a major grassland component (Reynolds and Linkhart 1987), however, indicates that this is not a requisite. It is not clear, however, that the size of the prey base has an impact on habitat choice in this species, as the preference for open physiognomy may be related to maneuverability and thermoregulation. The relationship between prey availability and reproductive success has not been investigated.

If the Flammulated Owl or Its Prey Rely on Particular Habitats, Are These Habitats Declining or Being Stressed by Current Management?

Because the habitat requirements of the flammulated owl appear to be best met in forests containing (but not limited to) yellow pines, and the vast majority of records of the species are from such forests, this section will assume that such forests are required for the survival of the species.

Global Climate Change

Global changes resulting in hotter and drier conditions in western mountains would presumably cause pine forests to migrate upslope. This would reduce the area of flammulated owl habitat and possibly extirpate the species from lower elevation mountain ranges, but sufficient habitat would likely remain to ensure the survival of the species (metapopulation structure would become more problematical; see below). A shift toward colder,

wetter regional climates would presumably shift the pine forests downslope and increase the area of favored habitat. Under this scenario, the species might pass through a population bottleneck until the new pine forest produced a sufficient inventory of snags and nest cavities. Warmer and wetter, or colder and drier, climates might produce a greater challenge for the owl because these are not equivalent to moving up or down existing montane climate gradients and the resulting plant associations are not predictable. It appears, from present knowledge of flammulated owl habitat, that increases in humidity are more likely to be deleterious than are decreases.

U. S. Forests Under Current Climatic Conditions

Western yellow pine forests are now intensively managed on public and private land and have changed radically in the past century (see Chapter 5). Although it is not known whether flammulated owl populations have increased or declined during this period, it is evident that the species has survived a dynamic interval in the history of its habitat. This fact is reassuring, but the specific components of its biology that enabled that survival remain unknown.

Flammulated owls evidently prefer old forests or at least structural characteristics associated with them. Such forests have declined drastically in extent (Chapter 5). The effect of total fire suppression would appear to have been undesirable for the owl, because it led not only to the proliferation of closed, even-aged stands of stagnant regeneration, but also to an increase in the frequency and intensity of catastrophic fires, which render an area unsuitable for decades to centuries. Data bearing directly on this hypothesis do not exist. Managed attempts to restore the presettlement physiognomy (e.g., thinning of thickets and controlled burning) appear to be beneficial to the owl, but once again data are lacking for testing this hypothesis. Logging, and especially firewood gathering, inevitably lead to a decrease in the inventory of snags, and this is an unqualified disadvantage for the flammulated owl.

Winter Range of Populations Breeding in the United States

No amount of attention to the flammulated owl in the United States will overcome loss of wintering habitat, presumably in southern Mexico. Mexican pine forests have been harvested with much the same abandon in the second half of this century that U.S. loggers employed in the first half. Fortunately for the flammulated owl, the USDA Forest Service bought up pinelands that had been clearcut by pri-

vate interests and engaged in massive reforestation. Whether similar reforestation occurs in Mexico may be the single most important factor in the long-term survival of the species.

Do the Life History and Ecology of the Flammulated Owl Suggest That Populations Are Vulnerable to Habitat Change?

Details of the life history strategy of the flammulated owl are incompletely documented, but the broad outline of the strategy is clear. This owl is a habitat specialist with low and unvarying fertility. These are adaptations to a stable environment. The only mechanism for dealing with declines in food supply during the breeding season appears to be reduction of the already small broods. Superabundance of food evidently does not lead to increased fertility, unlike some other owls, including the boreal owl. This "conservative" life history strategy, often referred to as K-selected, necessitates long life, i.e., high annual survival rates. K-selected bird species are typically large (which reduces risk of predation) and/or nonmigratory. The tiny, migratory flammulated owl therefore has an incongruous life history strategy, one that is fascinating for the theorist but worrisome for the conservationist. If habitat change causes small changes in survivorship that are not offset by concomitant increases in fecundity (which seems unlikely), the species could even now be on a slow but steady decline toward extinction. Sensitivity analyses of estimated life-history parameters suggest that survival of the species is indeed most sensitive to variation in adult survival. Concomitantly, the species appears to lack the high fecundity necessary to recover quickly from episodic population declines caused by human habitat alteration.

The environment of the flammulated owl has been anything but stable during the past century. Yet, as detailed above, the species seems to be holding its own. If this is not an illusion, it may have declined and rebounded (in which case its low fecundity is adequate to the task of dealing with habitat change), it may have increased in numbers, or it may have been unaffected by the kinds of change that have taken place. Genetic analyses of museum specimens and current populations would shed light on this question.

Metapopulation structure is another aspect of life history that may be influenced negatively by habitat change. A metapopulation is a large regional composite of smaller local populations that are linked

by dispersal. Populations restricted to mountaintops, such as those of the boreal owl in the southern part of its North American range, are classic examples of this type of population structure. Small population size carries with it the twin dangers of extinction owing to chance demographic events (e.g., unusually low overwinter survival), and genetic drift from loss of genetic variability and hence loss of adaptability. Frequent transfers among subpopulations obviate these problems and makes each small population part of a larger, more viable metapopulation.

The general habitat of the flammulated owl is continuous in some regions, e.g., the Mogollon Rim of Arizona, while highly discontinuous in others, e.g., isolated mountain ranges of Nevada, Utah, and southern Arizona. Some populations of this species are therefore probably not as susceptible to problems associated with small population size as others. Nevertheless, because natal dispersal distances are relatively great in most temperate zone bird species, most continuous populations probably have an underlying metapopulation structure, and undetected rescue events may occur frequently. Fragmentation of continuous habitat would then impose a more obvious and challenging metapopulation structure on such a species. When harvests of yellow pines involve selective cuts rather than clearcuts, avenues for dispersal should not be adversely affected by harvest regimes, even if recently harvested areas are unsuitable for nesting. Moreover, the (presumed) migratory nature of the flammulated owl may preadapt it to such situations, in that all members of this species presumably fly across areas of unsuitable habitat en route between their summer and winter quarters. Whether dispersing juveniles (which are the main agents of interpopulation movement in birds) are willing to do this during their late summer dispersal period is unknown.

The flammulated owl has been said by some authors to be semicolonial. Although the cause of the apparent clustering is more likely due to habitat heterogeneity than to social attractions or lack of dispersal ability, this phenomenon does imply a certain amount of population substructuring even in continuous habitat. If this is the case, some effects of small population sizes may already be felt by these clusters of birds. Fragmentation of habitat would exacerbate such a situation.

Is a Conservation Strategy Needed for This Species?

Current knowledge of the habitat requirements and life history strategy of the flammulated owl,

which is far from complete, suggests that the species is sensitive to habitat change and therefore likely to be in peril in the future given current land management practices. Because most habitat change in its current range is human-caused, a conservation strategy is needed to minimize or mitigate the effects of this change. The final details of such a strategy, however, cannot be formulated on the basis of current knowledge. Whether populations are secure or declining is not known, but the species currently occupies all of its known historic range in what appear to be good numbers. A crisis is not immediately at hand, and urgent measures are not needed.

It is my judgment that most of the basic information on population trends and habitat requirements necessary to fully determine the conservation status of the species and upon which to build a conservation strategy could be obtained in 5 years of coordinated research. Such information would greatly increase confidence in a long-term conservation strategy. A coordinated research program sufficient to obtain the most critical information is set out in the following section. Piecemeal research would be a terrible mistake.

While urgent measures presumably are not needed, prudence is called for during the proposed 5 years leading toward a conservation strategy. The implications of Chapters 4 and 5, and the direction proposed by the Payette National Forest (Chapter 3), provide a basis for management. In particular, biologists are encouraged: (1) to initiate nocturnal call surveys to detect areas of high owl density; (2) to identify large blocks of suitable habitat (i.e., mature to old ponderosa pine and mixed conifer forest) and initiate systematic nest searches; (3) to ensure retention and recruitment of snags in areas inhabited by flammulated owls for uneven-aged management in blocks of owl habitat; (4) to initiate studies in areas of high owl density to determine viability and habitat preferences; and (5) to support studies of flammulated owl biology as part of a coordinated effort within the Forest Service and with other agencies.

Management during this interim, and in the long run, must be coordinated among landowners across this species' broad distribution. As indicated in Map 1, only a portion of flammulated owl habitat occurs on National Forest lands. Coordination among managers of adjacent lands (e.g., Bureau of Land Management and Forest Service) and among managers across broad regions (e.g., Northern and Southwest regions of the Forest Service) will be a key to both managing and conducting research on this species. The USDI Fish and Wildlife Service's GAP analysis

program could play an important role in providing the information necessary to develop the coordination and cooperation.

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Information Needs: Flammulated Owls

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INTRODUCTION

Many kinds of basic information are required to devise a comprehensive and well-informed conservation strategy for this species. It is imperative that a unified, centrally directed approach be taken to obtain this information. Central oversight will make the effort more efficient and cost effective.

Here I assess the adequacy of existing knowledge to support the development of a conservation strategy and I point out specific knowledge gaps that need to be filled. I then describe a unified plan of research that would both provide the needed information and initiate a cost effective long-term monitoring system. The cost effectiveness of doing the necessary research now cannot be overemphasized. This species does not appear to be in immediate danger. Very thorough knowledge of virtually all aspects of its biology can be obtained for a fraction of the amount spent in a single year on an endangered species. Other high-interest forest species, as well as certain insect and plant groups, will also benefit from much of the proposed research.

STRENGTH OF EXISTING KNOWLEDGE TO FORMULATE A CONSERVATION STRATEGY

Throughout this section I approached each topic as a question. Is our understanding of this topic sufficient to support the development of a sound, national-scale conservation strategy for the flammulated owl? For example, "is the *distribution* of flammulated owls understood in sufficient detail to formulate regional conservation strategies?"

Distribution

Although systematic distributional surveys have not been conducted, enough has been learned from spotted owl surveys and other sources to delineate the range of the flammulated owl with reasonable confidence. The species is now presumed to occur

in all mid-elevation pine forests west of the Black Hills, as well as in a few other forest types. The initiation of regional conservation strategies is therefore justified throughout the western United States. Additional surveys are needed in order to delineate the range in the Oregon Cascades, in Washington, parts of Idaho, Montana, Utah, and Wyoming. Finer scale distribution, i.e., presence on individual Forests and Districts, is not as well understood but not necessary for formulating and implementing regional strategies.

Two aspects of distribution must be clarified, however, before regional strategies can be finalized. These are genetic variation and winter range. The distribution of genetic variation is completely undocumented. Modern studies, using molecular techniques, have not been performed, and subspecies described on the basis of coloration and clines in mensural characteristics are arbitrary and unrecognized by leading authorities (e.g., Marshall 1967, Voous 1989). A species-wide molecular survey of genetic variation would clarify the genetic structure of the U. S. populations and might identify the wintering grounds of well-defined northern populations. These winter ranges, which almost certainly lie in Mexico or farther south, must be discovered and their populations monitored. Otherwise, efforts to maintain the species in the United States could be pointless.

Response of Flammulated Owls to Stand-Level Habitat Changes

The virtual restriction of this species to middle elevations of semiarid mountain ranges is well documented, but the reasons for this habitat specificity remain undetermined. A study of flammulated owl thermoregulation, similar to Ligon's (1969) study of the other North American *Otus*, would indicate whether thermoregulatory constraints limit the upper and lower elevational ranges of the species. Moreover, studies of weight maintenance of provisioned captives kept in humidity and temperature

regimes similar to those of upper elevation conifer forests would show whether flammulated owls are capable of tolerating higher elevation forests when food supply is adequate. If such physiological constraints are absent then the limitation of flammulated owls to occupied habitats by food availability, competitors, and/or predators must be considered in management plans.

The response of flammulated owls to stand level habitat change is not understood definitively, but plausible hypotheses have been proposed and should be tested. Reynolds and Linkhart (1992) concluded from data gathered in Colorado that old yellow pine forests are preferred over younger stands for nesting territories, which encompass roosting and feeding as well as nesting per se. Assuming that preference for old forest is widespread, two important questions remain unanswered: (1) Do pairs in old forest have higher fitness (i.e., higher intrinsic rates of increase) than those in territories lacking old trees and other features of old forest? (2) Can the beneficial characteristics (e.g., openness, cavity abundance) of old forest be replicated with certain management treatments in younger forests? Answering these questions will require intensive study, including experimental habitat manipulation to determine the criteria by which flammulated owls choose nesting territories. Multilayered open canopies, with some shrub cover for foraging and dense conifer foliage for roosting, along with adequate nest cavities, are hypothesized to be the major requisites. A research program for studying each aspect of this hypothesis is described below.

Relationships with primary cavity nesters, with competitors (especially mammals), with insect prey populations, and with predators have not been studied quantitatively and require documentation. Of special concern is the European starling (*Sturnus vulgaris*), which is still in the process of invading flammulated owl habitat. Starling expulsion of flickers from old cavities (which is conjectured to be common) could actually lead to an increase in the number of flicker cavities, if it did not lead to the extinction of local flicker populations. Successful introduction of nest boxes to managed stands would remove dependency on primary cavity nesters and lessen the likelihood that unenforcability of snag regulations would lead to the loss of nest sites for the flammulated owl. But, if boxes along roads provided an avenue of population expansion for starlings, the boxes could do more harm than good. Which species would win a starling-flammulated owl contest for a cavity is a fact well worth obtaining, especially if nest boxes situated along roads become a major

research tool (see below). Van Woudenberg (1992) suggests that boxes may also attract flying-squirrels, which prey on flammulated owls (Cannings and Cannings 1982).

The relationship between flammulated owls and important insect prey populations are not understood. Furthermore, the role of forest structure and composition in determining the abundance and availability of prey is unknown. How these relationships vary geographically must also be understood in order to predict the consequences of stand management on flammulated owl fitness.

The effect of stand level changes on predators, competitors, and prey species is also potentially serious but will be difficult to gauge until the basic habitat relations of these target species are better understood. Correlational studies and modeling should be undertaken to produce first order approximations of the impacts of predators, competitors, and prey on viability of flammulated owl populations.

The fact that so many unknown factors play into the response of the flammulated owl to managed stand level changes argues for caution in implementing management alternatives that move stands away from presettlement physiognomy.

Effects of Broad-Scale Habitat Changes on Movement Patterns

Daily movement patterns appear largely limited to the owls' territories, which implies that changes in habitat on scales broader than forest stands will not affect within-year foraging success. Broad-scale changes may, however, affect within-year nesting success and survival by changing the mix of predators and/or competitors. Because breeding adult flammulated owls make extra-range movements during the nesting season, apparently to assess prospective mates and territories, broad-scale changes could have an impact on future nesting success. Attempting to evaluate these impacts in advance would be highly speculative.

Seasonal movement patterns evidently exist, but little is known of their extent. The phenomenology of natal dispersal of juvenile owls is barely known. Because a few radio-equipped juveniles have disappeared in August, while adults' radios continued to transmit, it may be hypothesized that natal dispersal takes place in late summer. Similar results have been obtained for the closely related eastern screech-owl (Belthoff and Ritchison 1989). These natal dispersal movements may traverse long distances, and hence may expose inexperienced owls

to dangers associated with crossing different habitat types, as hypothesized for the northern spotted owl (Gutierrez *et al.* 1985). The nature of such dangers for dispersing juveniles is not known.

All flammulated owls appear to migrate from nesting areas to wintering areas that are probably hundreds of kilometers to the south. The locations of these wintering areas are unknown. No conservation plan will be complete without knowledge of these locations and provision for threats posed by habitat change en route and in the winter quarters.

Relationship Between Foraging Behavior and Prey Abundance

The relationship between foraging behavior and stand structure has been described, but the relationship between variation in stand structure and foraging success has not been evaluated. Stand level change may affect foraging success by requiring owls to make less efficient maneuvers, which can have a large cumulative effect in a species that must capture many small prey items. Stand level change can also affect the prey base. Flammulated owls appear capable of using a wide variety of prey taxa, but the impacts of switching to alternative prey on reproductive success and adult survival have not been studied. Nor is it known if prey selection is as plastic and opportunistic as it appears. The documented regional variation in prey selection may represent local adaptation (i.e., evolved preferences) rather than opportunistic use of the locally most abundant members of a large prey pool. The impact of stand level habitat change on foraging success and nesting success therefore requires immediate study using experimental methods.

Comparison of published studies suggests that flammulated owls select prey opportunistically, and hence the owls do not engage in long-distance nomadic relocations in search of favored prey. The lack of nomadism, however, does not preclude a numeric response to prey fluctuation. Unpublished accounts of research conducted in British Columbia (St. John 1991, Van Woudenberg 1992) suggest a numerical response to a spruce budworm outbreak in that location, which is at the northern extreme of the owl's range. The New Mexico population studied by McCallum *et al.* (in review) fluctuated in numbers from year to year and showed little site fidelity, and hence may have been sensitive to prey numbers. The possibility that flammulated owls immigrate to areas experiencing outbreaks of forest insects should be investigated thoroughly.

Little is known of the population dynamics and

ecology of prey species. Because the flammulated owl is not a prey specialist, obtaining comprehensive information on prey dynamics will not be easy, but the task should be undertaken. Study of noctuid and/or orthopteran communities would be a desirable way to begin.

Demography

It is known that limited fecundity imposes constraints on the demography of the flammulated owl, but other key aspects of its demography are poorly documented. The gaps in knowledge prevent definitive statements concerning demographic persistence, and no population is known to be self-sustaining (i.e., independent of immigration). Detailed study will be required to evaluate persistence of local populations and metapopulations under alternative management plans.

Evaluating the impact of alternative management plans on demography will require at least the following basic information: (1) Estimates of adult annual survival, preferably age-specific survival. Because of the high site-fidelity at the Manitou study area in Colorado, available but as yet unpublished data on return rates from Reynolds and Linkhart's study can be used to estimate age-specific survivorship. (2) Estimates of survival from fledging to age 1. It will probably be necessary to divide this parameter into two multiplicative categories. Estimating dispersal success will require new radio-tracking studies on a spatial scale at least 10 times greater than the typical contiguous population study. Available technology is sufficient to the task. Estimating overwinter survival of first-year birds should first be attempted on the assumption that dispersing birds return in the following spring to locations selected at the end of their late-summer dispersal movement. This can be evaluated either by rechecking late-summer settling sites of juveniles used in the dispersal study or by banding a large number of immigrants to a contiguous-territory study area. (3) Estimates of dispersal distances. The dispersal study described above will yield this information, which is required for assessing the metapopulation structure of a region, e.g., a mountain range.

The purported clustering of territories also deserves statistical study. First, the reality of such clusters should be tested. Then their permanency should be assessed, and if confirmed, habitat variables should be measured inside and immediately outside the clusters. Simultaneously, owl productivity in and dispersal from the clusters should be assessed.

Monitoring Methods

Abundance is a potentially misleading indicator of population health (Van Horne 1983). Survival and/or successful nesting are the only dependable criteria of habitat sufficiency. Moreover, vocal survey methods for monitoring abundance are undependable because vocal activity varies with mating status and environmental factors. Unmated males are more likely to vocalize than mated males, and male presence is not an indicator of habitat sufficiency because unmated males may occupy suboptimal territories. Studies are needed to compare the characteristics of territories occupied by pairs and those occupied by males only.

More intensive methods are available for reliably evaluating the response of flammulated owls to management alternatives. The most reliable information would come from intensive population studies, with management treatments applied experimentally to old forest sites where the owls had been studied for several years. Nest box monitoring programs (Hayward *et al.* 1992) have the potential to produce acceptably reliable information on a shorter-term basis. Nest box programs can also provide a sounder basis for statistical inference.

Dynamics of Primary Plant Communities Used by the Flammulated Owl

Fortunately the ponderosa pine plant community has been studied in great detail, and predictive models are available for forecasting the habitat consequences, at least for tree species and grass species, of current management prescriptions. The dependence of flammulated owls on arthropods subsisting on shrubby vegetation is unquantified. Greater knowledge of the dynamics of this segment of the plant community may be required.

Historic Patterns of Distribution and Composition of Forest Communities Used by the Flammulated Owl

Are the historic patterns of distribution and composition of forest communities used by flammulated owls understood in sufficient detail to place current status in a historic context? The historic distribution of the flammulated owl, though poorly documented, appears likely to have been coextensive with the current distribution. Forest structure and community composition are also thought to be well understood for the pre-European period. It is not at all clear, however, how the flammulated owl responded

to the changes in its habitat over the past century. Whether the species is currently more or less abundant than before these changes is not known. The most critical information needed at present is whether current populations are viable or declining. Until such information is available, it should be assumed that current conditions are less favorable than were those before 1850. Policies with the goal of restoring present pine forests to presettlement physiognomy should be considered advantageous to the owl until the contrary is demonstrated. In order to clarify the relationship between forest composition and owl persistence, harvest of old yellow pine forest should be postponed, at least until before-harvest estimates of owl density and productivity can be obtained.

A RESEARCH PLAN

The information required to describe the conservation status of the flammulated owl falls into two categories that can be attacked with two different research strategies. In both cases, close coordination with Forest Service managers and researchers will be essential.

The first category is knowledge of the basic biology of the species, gaps that can be filled readily with short-term research projects. The second category is regional and continental trends in population dynamics, which should be designed and initiated by an experienced population biologist. A series of 16 nest box monitoring schemes, distributed throughout the range of the species in the United States, is recommended. Most data could be collected by local management personnel but should be analyzed and published in the peer-reviewed literature by an independent scientist. This approach will prevent charges of institutional bias in data analysis should the flammulated owl come under ESA at some time in the future.

A total of five short-term research projects is recommended for the owls. Useful research on competitors and predators is also outlined. These studies should be conducted by scientists having expertise appropriate to the research question, according to standard procedures. Some care should be given to conducting these studies at sites where appropriate habitat manipulations are underway or can be effected.

The continental project should be assigned to a scientist who can devote necessary time and attention to the conceptual development and interagency coordination required to set up a major continental monitoring scheme. It may be efficient to have a

single scientist in charge of all facets of Forest Service research on the three forest owls covered by this document. In the first few years most work effort would be devoted to coordination; later, after research projects are in place, this person could analyze data from monitoring schemes for all three species.

The research strategy recommended for assessing viability of the United States flammulated owl population is somewhat revolutionary. It departs from standard practice in that it emphasizes demographic parameters and de-emphasizes surveys and studies of abundance. It is unusual because of its spatial scale. Since the 1940's it has been standard practice among academic ornithologists interested in population biology to conduct intensive studies of local populations. These studies have yielded invaluable information on territoriality, extra-pair copulation, site-fidelity, variation in reproductive success, and other essentials of breeding biology, but the investment in effort required to conduct such a study has usually been made at the expense of replication. Such studies are often erroneously generalized to the regional population or even the species, when in fact the sampling design does not justify inferences beyond the local population from which the data were obtained.

Devising a regional or national conservation strategy for the flammulated owl requires obtaining information throughout the geographic region covered by the plan. Intensive study of contiguous territories, as informative as it is, cannot be replicated sufficiently to provide the required breadth of coverage. A nest box monitoring program described by Hayward *et al.* (1992) appears to offer an efficient strategy for gaining dependable information on the necessary spatial scale.

Nest box schemes appear to offer multiple benefits. They increase ease of access, allowing an increase in sample size over studies of contiguous territories. Placement can be partitioned among different habitat types, allowing assessment of habitat effects on a variety of performance categories (e.g., foraging success, nesting success). Finally, experience gained with them will be applicable to management efforts. Hayward *et al.* (1992) estimated that setting up a sufficiently large nest box monitoring system (approximately 300 boxes along existing roads in a single district, checked twice a summer by district personnel) would cost less than \$10,000 in material and labor. Annual maintenance and data gathering would cost less. Flammulated owls are not known for preferential use of boxes when cavities are available, but this may be due to particular pref-

erences for the placement of boxes. A pilot study could be undertaken to assess the preferences of these owls for box placement. If this study is successful, I would envision the establishment of 16 300-box systems throughout the range of the species in the United States. Three box studies would be conducted in the Pacific Southwest, Southwestern, Rocky Mountain, Intermountain, and Pacific Northwest Regions, and one in the Northern Region.

Information needs for devising national and regional conservation strategies have been synthesized into a series of coherent projects that are outlined below. A mere list could lead scientists to say that they can meet these needs with projects of their own conception. An efficient strategy requires that information needs be met in an integrated rather than piecemeal fashion. The nest box monitoring scheme comprises items III.A and III.B below. Several of the short-term projects can and should be done wholly or in part in coordination with this scheme.

Finally, the long-term population study being conducted by Richard Reynolds at Manitou Experimental Forest should be extended indefinitely. Not only has this study yielded the vast majority of the behavioral, reproductive, and ecological information presently available on the flammulated owl, it is the only study ever conducted over a time span sufficient to show population trends. Continuing this study would allow future comparisons of population dynamics with climate and habitat change. Reynolds' data alone are sufficiently detailed to allow estimation of vital rates now. The historical record of home range use at this study site would facilitate several of the graduate projects outlined below. Finally, a nest box network established in and adjacent to the study site would allow validation of the nest box project's assumptions and it would provide enhanced opportunities for detecting long-distance dispersal.

Outline of Suggested Research Projects

- I. REGIONAL VARIATION
Project conducted at a national center of excellence in systematics, with historical commitment to research in Mexico
- A. Modern morphometric study of existing specimens (coloration is not reliable because of fading)
- B. Assessment of genetic variation throughout the range of the species, using molecular techniques
- C. Identification of winter range of U.S. breeding populations
 1. Comparison of morphometric and molecu-

- lar data from United States and Mexico
 - 2. Field study of overlap of wintering and resident individuals, based on mist-netting or collecting
 - D. Taxonomic revision
- II. HABITAT REQUIREMENTS OF INDIVIDUALS
- A. Thermoregulatory capabilities — Short-term project (~2 years)
 - 1. Laboratory respirometry at different relative humidities and ambient temperatures
 - 2. Thermal properties of nest sites and roost sites in preferred, acceptable, and unoccupied home ranges. (Manitou Experimental Forest is best site because of long history of home range use)
 - B. Habitat selection by individuals — Experimental and observational study. Requires access to a Forest Service unit where habitat manipulations can be effected
 - 1. Contribution of floristics (i.e., food), structure (thermoregulation and foraging), and competition to preference for yellow pine
 - 2. Contribution of food, roost sites, and nest sites to preference for old forest
 - 3. Characteristics of bachelor male territories in comparison with pair-occupied territories
 - C. Familiarity with territory — Short-term project, best conducted at Manitou Experimental Forest because of long history of home range use, with comparative data from other populations (see III.)
 - 1. Contribution of age and familiarity with territory to foraging efficiency: observational and experimental
 - 2. Contribution of food abundance and foraging efficiency to reproductive success (including clutch size), including artificial provisioning
- III. VIABILITY OF SPECIES: POPULATION TRENDS AND VITAL RATES
- A. Trends (presence/absence repeated annually)
 - 1. Historic collecting sites
 - 2. Representative owl transects
 - B. Current viability in reference populations throughout U.S. range, using nest box networks that span stand types
 - 1. Annual variation in population size
 - 2. Vital rates, intrinsic rates of increase
 - 3. Immigration, emigration, net flux of individuals

- C. Cavity recruitment and availability
 - 1. Interspecific relations, including experimental study of ability of flammulated owls to usurp and hold cavities
 - 2. Modeling of competitor dynamics
 - D. Metapopulation structure — Coordinated short-term studies
 - 1. Based on molecular techniques
 - 2. Intensive study of dispersal in one population
 - 3. Modeling of metapopulation dynamics
- IV. COMMUNITY INTERACTIONS
- A. Community study of prey availability from April through October
 - B. Population dynamics of major prey species, e.g., noctuid moths
 - C. Comparative diet of bats and flammulated owls
 - D. Cavity competition between owls, other birds, and mammals

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Part III: BOREAL OWLS

Current Management Situation: Boreal Owls

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The range of boreal owls (*Aegolius funereus*) in the United States includes Alaska, the mountains of the western United States, and the northern tier states from the Atlantic to Pacific (see Chapter 9). Based on the species' documented distribution (see National Geographic Society 1987, Hayward *et al.* 1987, Johnsgard 1988, and others) the owl may occur on 81 National Forests across 7 Regions. To document the management status of the boreal owl throughout its range we queried management personnel on all National Forests where the species is likely to occur. Our questionnaire requested information on:

1. Documented breeding status of boreal owls on the National Forest (no records, recorded but breeding not confirmed, recorded breeding).
2. The range of habitats (by forest type) in which the species has been recorded on the Forest.
3. The existence of any Forest or Regional level conservation strategies and/or management plans.
4. The management status of the species in each Region (state list, USDA Forest Service-sensitive species list).
5. Whether forests are conducting distribution surveys for boreal owls.
6. The distribution of boreal owls plotted on a National Forest map, based on all data available from the Forest data base.

The questionnaire asked for additional, more qualitative, information. For instance, we asked how forests are addressing the needs of this species in biological evaluations (evaluating important habitat or population viability) and in monitoring plans. We were also interested in whether forests had information on changes in vegetation used by boreal owls over the last two centuries.

We also reviewed refereed literature sources for documented owl sightings and locations where museum specimens were collected. Most of these locations were plotted using U.S. Geological Survey 7.5" topographic maps. Where definite locations could be obtained they were plotted based on the latitude and longitude of the site. When locations were not clearly defined or described, the approxi-

mate center of the appropriate U. S. Geological Survey 7.5" topographic map was used. Forest Service source locations were plotted on 0.5-inch per mile Forest recreation maps using the same methods.

The distribution of boreal owls based on literature and agency locations is depicted in Map 2. This map also displays the combined potential distribution of subalpine fir (*Abies lasiocarpa*), balsam fir (*Abies balsamea*), Engelmann spruce (*Picea engelmannii*), black spruce (*Picea mariana*), and Sitka spruce (*Picea sitchensis*) — forest types where boreal owls most commonly breed (see Chapter 9). Vegetation boundaries were derived from Kuchler's potential natural vegetation (Kuchler 1964) for the region south of Canada and from Burns and Honkala (1990) for Alaska. The owl locations and vegetation distribution were digitized and plotted on an existing map of the United States.

Boreal owls were reported to occur on 43 of the 81 forests where the species may be expected. The owl has been recorded breeding on 13 of these forests. The boreal owl is listed as a USDA Forest Service sensitive species in four regions and on one additional forest (Superior National Forest) in a region where the species has no regional status (table 1). Despite these special management designations, specific forest or regional level management plans have been written for only two Forests (Tongass and Superior National Forest). General raptor management guidelines or general statements concerning nest protection have been written on the Willamette National Forest and these refer to the boreal owl in a general way. Management on the Superior National Forest provides for managing 200-acre tracts of black spruce for the boreal owl as an indicator species. On the Tongass National Forest, management direction indicates (Suring 1993, our synopsis):

1. Establish Habitat Conservation Areas (HCAs) of old-growth forests 5,000 acres in size or larger. These HCAs should be approximately 10 miles apart edge-to-edge and distributed across the landscape. Each block would provide habitat for 1 to 13 pairs of boreal owls.

2. An alternative strategy would be:
 - a. Manage the 5,000 acre HCAs allowing low intensity timber harvest (i.e., maintain 60% of the old growth and harvest 40% using group selection).
 - b. Provide an additional 5,000 acres of old-growth forest for travel corridors between blocks with moderate intensity timber harvest (i.e., maintain 40% old-growth and harvest 60% using group selection).
 - c. Manage the remainder of the watershed under intensive forest management (i.e., clearcut).
3. When individual nests are found outside of the HCAs, they should be protected with a half-mile buffer, thus providing approximately 500 acres of habitat adjacent to the nest.

Although many forests report the presence of boreal owls, there is little information on population or habitat trends. In those Regions where the boreal owl is classified as "sensitive," distribution surveys targeting this owl are being conducted and distribution information should improve over time.

In addition to its designation as a sensitive species by the USDA Forest Service, boreal owls are given special management status in three states: Idaho (Species of Concern), Montana (Species of Concern), and Washington (to be monitored). Breeding status has only recently been established in many states; therefore, other state designations may be forthcoming.

The response we received from National Forests throughout the range of boreal owls indicates that little is known about the species in these management units (table 2). Furthermore, there is no mechanism in place to gather much of the data necessary for management. On Forests where some attempt has been made to manage boreal owls or raptors in general, there appears to be little scientific basis for

their management.

The status and trend of subalpine and aspen forests throughout the range of the boreal owl is critical to assessing the species' current management status. During the time available to produce this report we were unable to accumulate accurate information necessary to infer changes that have occurred and can be expected to occur in forests used by the species. We feel this information is important, however, and our interest in understanding the status and ecological trends of important forest habitats is reflected in Chapter 10 of this report.

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Table 1.—Status of the boreal owl on National Forests as reported by managers in early 1993.

Region	No. of Forests in Region	No. of Forests where owl is present	No. of strategies or plans in place	Addressed in Forest management plan?	Forest Service conservation status
Northern	13	13	None	No	Sensitive
Rocky Mountain	12	10	None	No	Sensitive
Southwestern	11	2	None	No	Sensitive
Intermountain	16	7	None	No	Sensitive
Pacific Southwest		Not reported in this Region			
Pacific Northwest	19	6	None	1 forest	None
Eastern	14	1	None	1 forest	None
Alaska	4	4	3	No	None

Table 2.—Habitat associations of the boreal owl based on surveys of USDA Forest Service data bases. Habitat is described by dominant overstory tree species: SF - Spruce-fir forest, LP - Lodgepole pine forest, DF - Douglas-fir forest, ES - Engelmann Spruce forest, MC - Mixed conifer forest, PP - Ponderosa pine forest, QA - Quaking aspen forest, MH - Mountain hemlock forest, RF - Red fir forest, BS - Black spruce forest. Status for National Forests who did not respond is listed as "not present."

State	Forest	Occurrence	Habitats
Northern Region (Region 1)			
Montana	Beaverhead	Breeding	>8000 ft., SF, LP
Montana	Bitterroot	Present	>5300 ft., SF, LP
Idaho	Idaho Panhandle	Present	>5000 ft., SF
Idaho	Clearwater	Breeding	>4000 ft., LP
Montana	Custer	Present	~7000 ft., SF, LP
Montana	Deerlodge	Present	LP, DF
Montana	Flathead	Present	>5500 ft. SF
Montana	Gallatin	Present	LP, SF
Montana	Helena	Present	>5000 ft., SF, LP
Montana	Kootenai	Present	>5000 ft., SF
Montana	Lewis and Clark	Present	6400-8400 ft., SF, DF
Montana	Lolo	Breeding	Mature, Old SF, DF
Idaho	Nez Perce	Present	~6300 ft., SF, DF
Rocky Mountain Region (Region 2)			
Wyoming	Bighorn	Present	
South Dakota	Black Hills	Not present	
Colorado	Grand Mesa etc.	Present	SF, LP, MC
Wyoming	Medicine Bow	Suspected	
Colorado	Rio Grande	Breeding	SF
Colorado	Arapaho/Roosevelt	Breeding	SF Old Growth
Colorado	Routt	Suspected	SF, LP
Colorado	Pike/San Isabel	Suspected	SF, ES
Colorado	San Juan	Present	SF
Wyoming	Shoshone	Present	
Colorado	White River	Present	
Nebraska	Nebraska	Not present	
Southwest Region (Region 3)			
Arizona	Apache/Sitgreaves	Not present	
New Mexico	Carson	Present	SF
New Mexico	Cibola	Not present	
Arizona	Coconino	Not present	
Arizona	Coronado	Not present	
New Mexico	Gila	Not present	
Arizona	Kaibab	Not present	
New Mexico	Lincoln	Not present	
Arizona	Prescott	Not present	
New Mexico	Santa Fe	Present	SF
Arizona	Tonto	Not present	
Intermountain Region (Region 4)			
Utah	Ashley	Present	
Idaho	Boise	Present	SF Over 6000 ft.
Wyoming	Bridger-Teton	Breeding	MC, LP
Idaho	Caribou	Present	DF, SF, LP
Idaho	Challis	Not present	

Table 2 - (continued),

Utah	Dixie	Not present	
Utah	Fishlake	Not present	
Nevada	Humboldt	Not present	
Utah	Manti-La-Sal	Not present	
Idaho	Payette	Breeding	SF, PP, DF, QA
Idaho	Salmon	Breeding	SF
Idaho	Sawtooth	Present	
Idaho	Targhee	Breeding	LP, DF, QA
Nevada	Toiyabe	Not present	
Utah	Uinta	Not present	
Utah	Wasatch-Cache	Suspected	

**Pacific Northwest Region
(Region 6)**

Oregon	Deschutes	Present	MH, RF
Oregon	Fremont	Not present	
Washington	Gifford Pinchot	Not present	
Oregon	Malheur	Not present	
Washington	Mt. Baker	Not present	
Oregon	Mt. Hood	Not present	
Oregon	Ochoco	Not present	
Washington	Okanogan	Breeding	
Washington	Olympic	Not present	
Oregon	Rogue River	Not present	
Oregon	Siskiyou	Not present	
Oregon	Siuslaw	Not present	
Oregon	Umatilla	Present	
Oregon	Umpqua	Not present	
Oregon	Wallowa-Whitman	Present	
Washington	Wenatchee	Present	
Oregon	Willamette	Present	
Oregon	Winema	Not present	
Washington	Colville	Not present	

**Eastern Region
(Region 9)**

Wisconsin	Chequamegon	Not present	
Minnesota	Chippewa	Not present	
Michigan	Huron-Manistee	Not present	
Missouri	Mark Twain	Not present	
Wisconsin	Nicolet	Not present	
Michigan	Ottawa	Not present	
Illinois	Shawnee	Not present	
Minnesota	Superior	Breeding	Lowland BS
Michigan	Hiawatha	Not present	
Pennsylvania	Allegheny	Not present	
Vermont	Green Mt.-Finger Lake	Not present	
West Virginia	Monongahela	Not present	
New Hampshire	White Mountain	Not present	
Indiana	Wayne-Hoosier	Not present	

**Alaska Region
(Region 10)**

Alaska	Tongass-Stikine	Present	
Alaska	Tongass-Chatham	Present	
Alaska	Chugach	Present	
Alaska	Tongass-Ketchikan	Present	

Review of Technical Knowledge: Boreal Owls

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INTRODUCTION

The boreal owl (*Aegolius funereus*), known as Tengmalm's owl in Eurasia, occurs throughout the holarctic in boreal climatic zones. This medium-size owl (100-170 g) occupies boreal and subalpine forests in an almost continuous circumboreal distribution that extends from Scandinavia eastward across the northern forests of Siberia and from Alaska across Canada to the Atlantic (Dement'ev and Gladkov 1954). On each continent, disjunct populations occur in mountains south of the broad transcontinental boreal forest populations (Cramp 1977, Voous 1988). Boreal owls in the mountain regions of Europe and Asia have long been recognized as isolated resident breeding populations, whereas in North America, breeding status was only recently documented in the mountains of the western United States (Hayward and Garton 1983, Palmer and Ryder 1984, Hayward *et al.* 1987a, Whelton 1989).

In-depth study of boreal owl biology and ecology in North America is limited to four, short-term investigations (Bondrup-Nielsen 1978, Meehan 1980, Palmer 1986, and Hayward *et al.* 1993). As an example of the lack of attention paid this species, prior to 1979 the USDI Fish and Wildlife Service had no records for banded boreal owls west of the Mississippi (W. Martin, pers. comm.). Knowledge of the species' biology and ecology comes mostly from Fennoscandia where *Aegolius funereus* may be the most studied owl. Many investigations in Europe are long-term efforts. Franz *et al.* (1984), Sonerud (1989), Schelper (1989), and Korpimaki (1992) each report studies lasting over 15 years. Korpimaki, who initiated investigations in 1966, continues work on the same sites today. Ecologists in Fennoscandia and eastern Europe have emphasized study of breeding biology, productivity, movements, food habits, and relationship with prey populations. These studies stem largely from examination of populations that breed almost exclusively in nest boxes. Results from studies in the Old World indicate that the biology and ecology of boreal owls vary geographically and

are strongly related to local forest conditions and prey populations.

In contrast with studies in Europe, habitat use has been emphasized in the few investigations in North America. Studies on the two continents have generated few data with which to contrast the biology of the species between continents. Therefore, the basis for inferring North American biology and ecology based on European results is unclear. The variability witnessed in Europe suggests caution. However, to the degree that variation in Europe follows geographic, climatic, or habitat gradients, a more sound basis upon which to build inferences for North America is possible.

The paucity of scientific knowledge from North America necessitates reliance on the extensive knowledge accumulated in Europe for portions of the assessment. Ignoring that knowledge would be careless. However, we cannot directly infer ecological patterns in North America based on the European knowledge. Therefore, I have been careful to point out the geographical source of knowledge, and where appropriate, describe ecological patterns for Europe that have been related to environmental gradients. By doing so, I seek to describe patterns recognized in Europe that may relate to populations in North America.

Note: Throughout this paper, measures of variation are 95% bounds on estimates unless otherwise indicated.

SYSTEMATICS

Ford (1967) associated the genus *Aegolius* with *Surnia* and *Ninox* (northern and southern hawk owl genera) based on osteology of 75 owl species. Aside from the boreal owl, the genus *Aegolius* includes three species: the northern saw-whet owl (*A. acadicus*), unspotted saw-whet owl (*A. ridgwayi*), and buff-fronted owl (*A. harrisi*), which all occur only in the New World. The largest species of the genus, *A. funereus* occurs north of the others and is more widely distributed. Norberg (1987) speculates that

the genus originated in the New World and only the boreal owl expanded its range beyond the Americas. The more northern distribution and larger size of *A. funereus* likely facilitated range expansion via the Bering Strait.

Boreal owls in North America represent a homogeneous taxonomic group and are recognized as a single subspecies, *A. funereus richardsoni*. Six subspecies are recognized in Eurasia. Abrupt distinctions are apparent in only *A. f. beickianus* and *caucasicus*, which are southern, more isolated populations. Otherwise, *A. f. funereus* — north and central Europe; *A. f. sibiricus* — north and central Asia; *A. f. magnus* — northeast Siberia; and *A. f. pallens* — west and central Siberia vary as a cline across Eurasia (Dement'ev and Gladkov 1954). Generally the largest and lightest forms are found in northeast Siberia, with a size reduction and darkening westward and southward (Dement'ev and Gladkov 1954). *A. f. richardsoni* is among the darkest forms.

DISTRIBUTION

Species Range

Boreal owls occupy boreal forests throughout the northern hemisphere forming an almost continuous band across North America and Eurasia. In Europe, scattered populations extend south of the circumboreal range in the Pyrenees, Alps, and Caucasus mountains and in Asia along Tarbagatai, Tien Shan, and Zervshan ranges (see maps in Dement'ev and Gladkov 1954:436 and Cramp 1977:607, 608 for worldwide distribution). Similar southern populations occur in North America as described below.

Recently the species' documented range has expanded in Europe like in North America. Most new records are from mountainous locales (see Cramp 1977:607 and Hayward *et al.* 1987a). Rather than a recent range expansion, these records likely represent increased interest in owls and increased human recreation in mountain areas during winter.

North America

Within North America, boreal owls occur in a continuous band concurrent with the boreal forests of Alaska and Canada (see Johnsgard 1988 for continental distribution). The breeding range extends from northern treeline southward in forested regions of Canada to the extreme northern United States in Minnesota (Eckert and Savaloja 1979, Lane 1988) and likely Wisconsin (Erdman 1979), Michigan, and

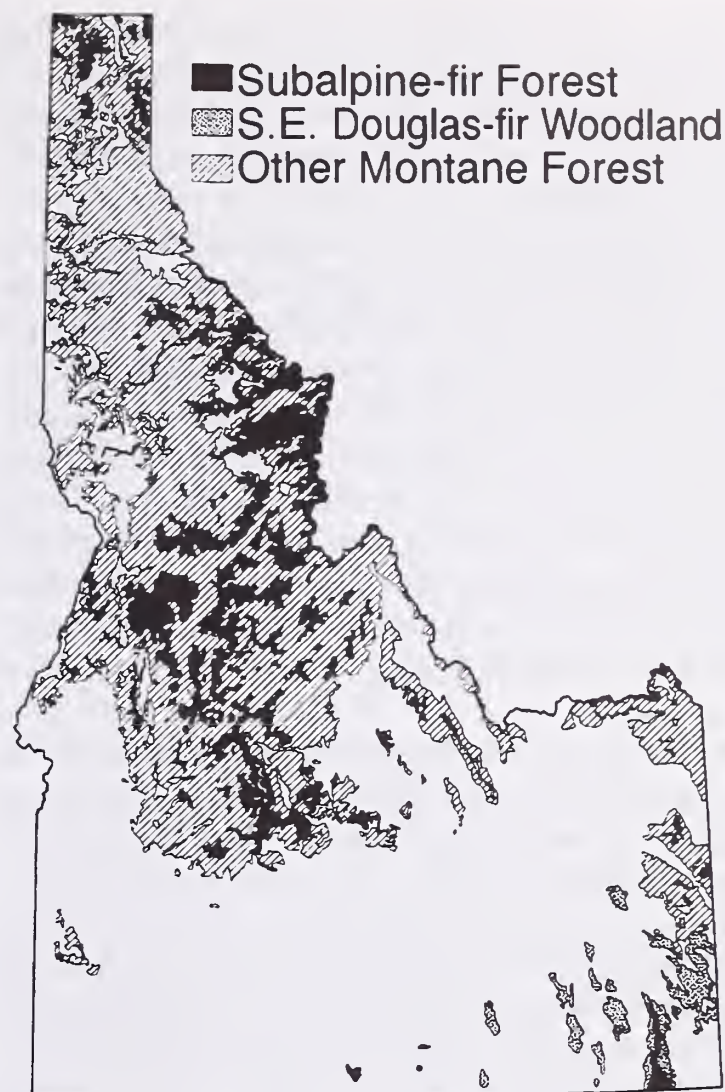


Figure 1.—Example of the patchy nature of boreal owl distribution in the western United States based on the species' estimated distribution in Idaho. Owl distribution inferred from distribution of forest vegetation types. Potential habitat is defined as forested sites in the subalpine-fir zone throughout the state and Douglas-fir woodland in southeastern Idaho. Other montane forests are not considered potential habitat. Data taken from Idaho gap analysis project (adapted from Hayward *et al.* 1993).

Maine (Catling 1972). East of the Rocky Mountains, breeding has been confirmed only in Minnesota. In western North America the species' range extends southward beyond 38° N latitude (Map 2). South of the continuous transcontinental band, populations are restricted to subalpine forests in the Rocky Mountains, Blue Mountains, and Cascade Ranges (Palmer and Ryder 1984, Hayward *et al.* 1987a, Whelton 1989). The southernmost records occur in mountains of northwestern New Mexico (Stahlecker and Rawinski 1990).

Due to the species' association with high elevation forests in the western United States (discussed in-depth under Habitat Use), populations may occur as geographic isolates dispersed throughout the western mountains (for an example see figure 1). As a result of the naturally fragmented nature of boreal owl habitat in the western mountains, the species is distributed in North America in two contrasting patterns. In the north, populations of interacting in-

dividuals may extend for hundreds of miles, while in the south, numerous breeding populations occur as islands of habitat linked only through long-distance dispersal through extensive areas without breeding habitat.

Although boreal owls are thought to breed in much of the forested portion of Alaska, surveys have been conducted in few portions of the state (see Gabrielson and Lincoln 1959, Armstrong 1980). Literature documentation for boreal owls in Alaska extends from the Brooks Range (Campbell 1969), to the Pribilof Islands (Evermann 1913), and to the north Gulf Coast (Isleib and Kessel 1973). Recent surveys document singing boreal owls in southeast Alaska on the mainland and a number of islands (draft agency report, Suring 1993; see Map 2 in sleeve of this book).

The recognized distribution of boreal owls has changed yearly since 1979 as interest in the owl developed and efforts to locate breeding populations increased. Prior to 1979, breeding populations of boreal owls were not thought to occur south of Canada. The 1983 American Ornithological Union checklist of North American birds described the southern extent of western boreal owl populations as south-central Canada, although it also recorded breeding populations in Colorado and northwestern Wyoming. In 1985, Idaho, Washington, and Montana were added (data reported in Hayward *et al.* 1987a) but populations were recognized in only isolated locales in each state. By 1987, biologists realized that populations occurred throughout the northern Rockies in high elevation conifer forests south to northern New Mexico. I expect the documented range to continue to expand as previously unsurveyed regions receive attention. In Idaho and Montana, where surveys have been conducted for over a decade, our understanding of boreal owl distribution will become more refined. In regions where few surveys were conducted in the past, such as Utah, Alaska, northern Wisconsin, northern Michigan, and northern New England, I expect significant changes in the recognized distribution.

Map 2 depicts the estimated breeding range of the species based on reports from the literature and recent surveys conducted largely by state and federal agencies. Reports from the technical literature are acknowledged separately from agency surveys, because these records have undergone greater scrutiny. I recognize that individual records may be suspect.

Some surveys were conducted by inexperienced persons and the level of training and experience of personnel conducting surveys varied. Because the majority of survey personnel received some training and discussed their observations with owl experts, however, I believe the estimated distribution to be reliable.

Species Status and Trend

Direct measures of population status or trend are not available for populations in North America. In contrast with Europe, investigations of boreal owls in North America have been short term and have not emphasized study of productivity or demography. Due to the paucity of historical information, direct estimates of status and trend will be difficult in the near future. Currently, I am aware of only one effort, begun in 1988, to intensively monitor population trend in North America (Hayward *et al.* 1992).

The boreal owl's range in North America is extensive. In northern Canada, it occurs in many areas where land management currently does not alter natural vegetation patterns. Recent surveys indicate the species also occupies an extensive geographic range south of Canada. Populations in this region occur on lands where human impact is greater. The potential influence of land management on owls across these lands will be discussed later in this document. Since direct measures of trend are not available, and the species occupies a large geographic area, any inferences to population trend must be inferred indirectly by linking the species' ecology and observed patterns of landscape change.

In Fennoscandian forests, boreal owls are considered the most abundant Strigiform (Merikallio 1958, cited by Korpimäki 1984). Despite long-term investigation of the species, however, reliable indication of long-term trends are unavailable due to the difficulty in surveying and censusing nocturnal owls (Lundberg 1978). Short-term fluctuations in breeding populations are evident from nest box surveys (e.g. Franz *et al.* 1984, Lofgren *et al.* 1986, Schelper 1989, Sonerud 1989, and Korpimäki 1992), but status and long-term trends have not been reported. Significant reduction in natural breeding cavities in Scandinavia resulting from removal of old forest (Korpimäki 1981 and others) would imply reduced populations and potentially restricted distribution.

MOVEMENTS: ANNUAL, SEASONAL, AND DAILY

Annual Movements and Site Tenacity of Adults

Annual movement patterns of boreal owls are poorly understood in North America but have received considerable attention in Fennoscandia and Germany. Trapping stations at Whitefish Point, Michigan, and Hawk Ridge Research Station, Minnesota, and records of owl sightings by birders represent the majority of data on boreal owl movements in North America (Kelley and Roberts 1971, Catling 1972, Evans and Rosenfield 1977 and references therein). Trapping observations are difficult to interpret, and conclusions drawn from these observations must be regarded as hypotheses.

Based on the periodic sightings of boreal owls (1922, 1954, 1962, 1965, 1968) south of the species' range in eastern North America, winter irruptions have been hypothesized by Catling (1972) and Evans and Rosenfield (1977). Reported irruptions extend from Maine through Michigan and Minnesota (Catling 1972). Periodic observations of boreal owls have been documented in Illinois (Coale 1914, Wyman 1915), Minnesota (Evans and Rosenfield 1977), Wisconsin (Erdman 1979), and New York (Yunick 1979) and frequently coincide with increased observations of northern saw-whet, great gray (*Strix nebulosa*), and northern hawk owls (*Surnia ulula*). Sightings and captures are concentrated in autumn (late October-mid November) and late winter (February-April). The age and sex composition of the irruptive populations are poorly understood. Furthermore, whether individuals observed during these irruptions attempt to breed in southern areas, return to breeding areas in the north, or represent a population sink, is unknown. Catling (1972:223) suggests that a return flight occurs in April and May. Speculation concerning direction of movements appears to be based on little empirical evidence.

In Idaho, during a single week in February 1986, two radio-marked males left home ranges occupied for more than a year (a third male died during the same period). One male was relocated in May 80 km away. Three radio-marked females in Idaho left their former home ranges within 2 weeks of ceasing brooding young in July. One moved ~17 km while the others moved greater distances and could not be relocated (Hayward *et al.* 1987b). Although these owls were documented making nomadic-like movements, other radio-marked owls in the study re-

mained sedentary. These observations are very limited but suggest nomadic behavior.

In contrast with limited information in North America, extensive European studies suggest a complex pattern of nomadism and site tenacity that varies geographically and differs among sex and age classes. In general, the species is characterized as nomadic, at times exhibiting year-round residence within a stable home range but dispersing in years of poor prey populations (Myserud 1970, Wallin and Andersson 1981, Lofgren *et al.* 1986, Korpimäki *et al.* 1987, Sonerud *et al.* 1988, Schelper 1989). Korpimäki (1986b) recognized a trend of increased population fluctuations in more northern populations associated with a greater degree of nomadism. He related the pattern to winter snow depth and range of prey available to the owls in winter.

In Scandinavia where year-to-year movements were studied using band recoveries from long-term site specific studies employing nest boxes, a unique pattern of residency and nomadism was first recognized by Myserud (1970). Myserud (1970) suggested that nomadic behavior in the Fennoscandian population is adapted to the 3-4 year microtine cycle and regional variability in microtine abundance. Lundberg (1979) refined the model and hypothesized that the conflicting pressures of food stress favoring nomadism and nest site scarcity favoring site tenacity result in different movement patterns in males and females; females exhibit nomadism while males exhibit greater site tenacity. Lofgren *et al.* (1986), Korpimäki *et al.* (1987), and Sonerud *et al.* (1988) confirmed the mixed pattern of male residency and irregular female dispersal in adult Tengmalm's owls. Korpimäki's review (1986b) further refined the understanding of nomadism in the species, suggesting that sexual differences in residency vary geographically. In central Europe both sexes appear to be largely site tenacious, but young owls are nomadic (Franz *et al.* 1984). In southern Fennoscandia males are resident and females and juveniles nomadic. In northern Sweden, both adults and juveniles exhibit nomadism (Korpimäki 1986b).

In addition to the influence of snow conditions, geographic setting, and prey conditions mentioned above, nest predation and nesting success have been shown to influence dispersal in adult female boreal owls (Sonerud *et al.* 1988). Adult females whose nests are unsuccessful have an increased probability of dispersing long distances. Predation of nestlings further increases the probability of long dispersal (figure 2).

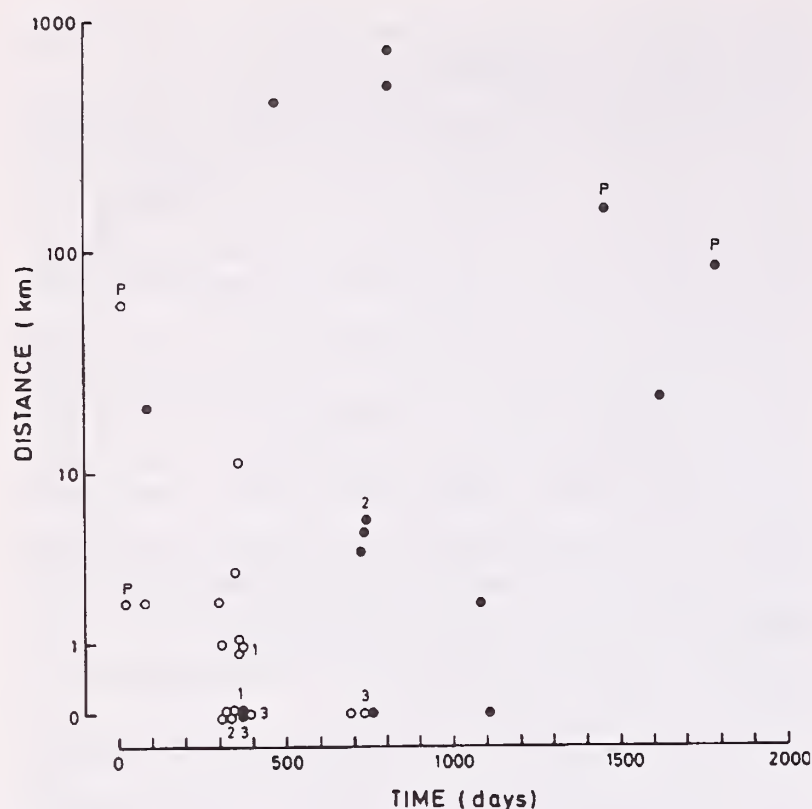


Figure 2.—Distance moved and time elapsed between ringing and recovery of female Tengmalm's owls ringed in Norway while breeding. Open circles denote dispersals occurring within a microtine peak (high prey availability), and filled circles denote dispersals involving a microtine decline (low prey availability). Dispersals following nest predation are indicated by a P. Dispersals made by the same female are indicated by numbers (from Sonerud *et al.* 1988).

Dispersal Frequency

Interpopulation movements are extremely important in metapopulation (population of populations) dynamics. Therefore it is important to determine rates of immigration and emigration among component populations. Estimating the portion of a population involved in nomadic or dispersal movements is difficult, however. For instance, most recoveries of banded birds are from nesting birds re-trapped by the original bander. Therefore, estimates of dispersal will be biased toward documenting site tenacity or short-distance movements.

Despite these shortcomings, studies of boreal owls in Fennoscandia and Germany have estimated emigration rates that follow the north-south geographic gradient described earlier (more nomadic movements in northern populations). After successfully nesting, 0% and 8% of adult females dispersed farther than 20 km from two populations in Germany (central Europe) (Franz *et al.* 1984 and Schwerdtfeger 1984, both according to Sonerud *et al.* 1988). Corresponding proportions for central Norway, Finland, and northern Sweden were 14%, 31%, and 33%, respectively (Lofgren *et al.* 1986, Korpimaki *et al.* 1987, and Sonerud *et al.* 1988). The proportion of adult females dispersing farther than 100 km in central Norway, Finland, and northern Sweden were 13%, 17%,

and 17%. In all cases dispersal over 100 km took place between microtine peaks.

Proportions of males dispersing is more poorly documented because of the greater difficulty in trapping nesting males. In one Finnish study (Korpimaki *et al.* 1987), all re-trapped males ($n = 23$) were caught within 5 km of the original banding site. Of 170 males recovered in Finland, only two have been recovered far from their original breeding site (97 and 180 km).

Based on these patterns, I suggest that boreal owls in the United States likely occur in a metapopulation structure. The nomadic nature of the species, frequent movements by adults and young, and the ability of individuals to disperse long distances indicate the species' behavior facilitates a metapopulation distribution. Furthermore, suitable habitat in the United States occurs in numerous patches separated by tens to hundreds of km (figure 1, also see *Movements as Related to Demography and Metapopulation Structure* later in this chapter). The habitat distribution, then, provides a landscape that will support small populations each separated by distances greater than the normal daily movement and normal yearly movement distances of individual owls. Linkage among populations, then, results from the nomadic movement of adults or exceptional long-distance dispersal of some young owls.

Dispersal Distances

Adults who disperse over 20 km from a breeding site may frequently move long distances as nomads. Documenting long movements is difficult, however. Lofgren *et al.* (1986) reported females breeding 550, 308, 289, 220, 70, and 70 km from their original breeding site in northern Sweden. In the same study, Lofgren *et al.* (1986) reported males breeding 21 and 115 km from their original breeding site. Sonerud *et al.* (1988) reported dispersal distances for breeding adult females first banded in southeastern or central Norway (figure 2) while Korpimaki *et al.* (1987) summarized dispersal distances for Finland (figure 3). In Germany, based on owls banded at nest boxes, Franz *et al.* (1984) found 5% of females nesting in the same box as the previous year and that the shortest 93% (left side of the distribution) of all dispersal movements averaged 9.3 km. Of the 2% of females who dispersed long distances, the maximum was 194 km. Other maximum distances include 728 km for Norway (Sonerud *et al.* 1988), 550 km for Sweden (Lofgren *et al.* 1986), and 550 km for Finland (Korpimaki *et al.* 1987).

Annual Movements and Site Tenacity of Juveniles

Young boreal owls frequently disperse long distances from natal sites but have been recorded breeding within 0.5 km of their natal site (Hayward, G. D. and P. H. Hayward unpublished data from Idaho). Korpimäki *et al.* (1987) reported median distances of 88 and 21 km between juvenile male and juvenile female banding sites and later at two breeding sites in Finland (figures 3 and 4). In Norway, 3 males banded as juveniles were recaptured breeding 5-11 km from the natal site while 9 females had moved 2-239 km (Sonerud *et al.* 1988). Twenty percent of recoveries for owls marked as nestlings exceed 100 km in West Germany (Franz *et al.* 1984) and 51% in Finland (Korpimäki *et al.* 1987).

Seasonal Movements

Patterns of movements associated with seasonal cycles have been studied in only one locale (Hayward *et al.* 1993). Patterns observed during this study in the wilderness of central Idaho may be unique to the geographic characteristics of the study area. Winter and summer home ranges of individual owls overlapped extensively but centers of activity for 12 radio-marked owls shifted. Average elevation of roosts used by the owls was 186 (± 105) m lower in winter than summer. Despite this shift, areas used in winter had complete snow cover exceeding 0.5 m each winter and the owls frequently used areas with 1.5-2.0 m of snow accumulation. Snow-free slopes occurred within 2 km of most owls' ranges during most winters, but owls were not observed using these areas.

Movements Within the Home Range

Burt (1943:351) defined home range as the area traversed by an individual in its normal activities of food gathering, mating, and caring for young. For boreal owls, these movements define how individuals use space during periods when they are not nomadic or dispersing. Except during periods of nomadism, boreal owls are resident within and between years.

Boreal owls studied in the western United States use large home ranges. In Colorado, home ranges of two males located on daytime roosts (>8 locations for each owl spanning 252 and 173 days) encompassed 1,395 and 1,576 ha and overlapped one another by >90% (Palmer 1986). In central Idaho, nest sites occurred in lower portions of home ranges (few

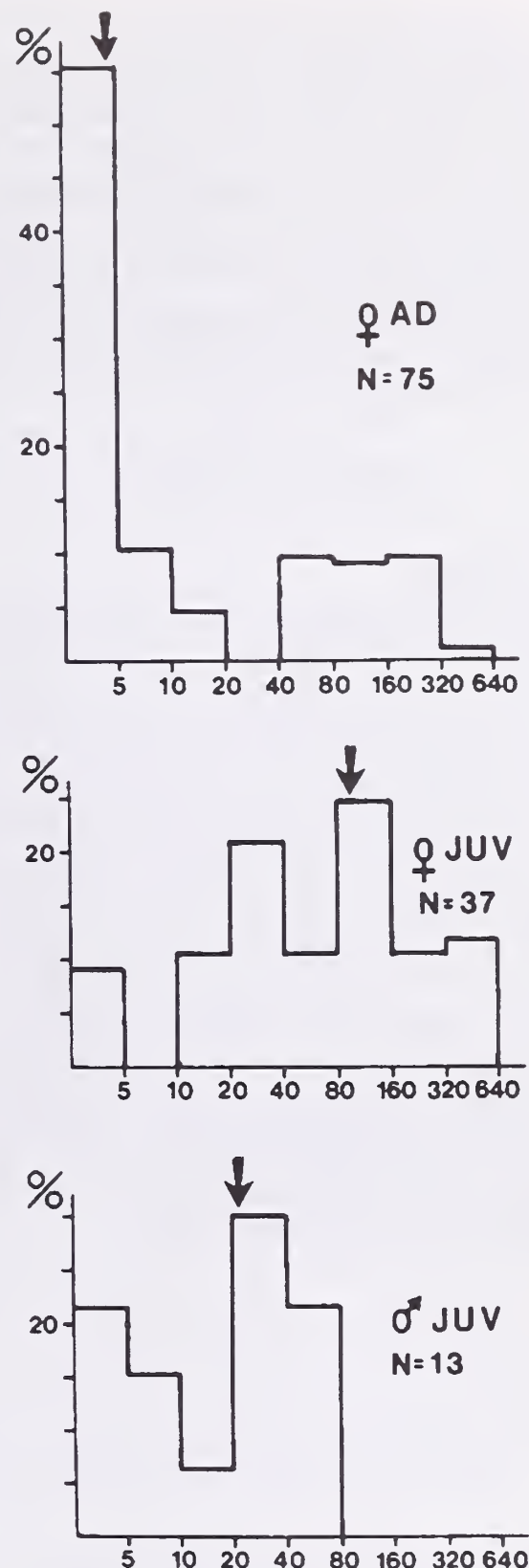


Figure 3.—Dispersal distances (km, log scale) between ringing and recovery sites of Tengmalm's owls ringed as breeding females (upper chart) or nestlings (lower charts) and retrapped in later years when breeding. Medians (4 km, 88 km, and 21 km) are indicated by arrows. N = number of recoveries (from Korpimäki *et al.* 1987).

cavities were found at higher elevations) while roosting and foraging occurred throughout the range. Winter ranges covered 1,451 ha (± 522 ; $n = 13$, range 320-3390 ha), and summer ranges covered 1,182 ha (± 334 ; $n = 15$, range 229-2386 ha). These estimates of home range size are based on modest sample sizes and therefore should be considered minimum use areas. Harmonic mean estimates (which were used in this case) tend to be biased low with small sample

size (E. O. Garton; pers. comm.).

Boreal owls are very mobile predators; the owls frequently traverse much of their home range in the course of 2-3 days or weeks (Hayward *et al.* 1987b). In spruce-fir forests of Colorado, roosts used on consecutive days averaged 708 m apart ($n = 113$) (Palmer 1986). In Idaho, distance between consecutive roosts of 14 owls (150 locations of consecutive roosts) averaged 1,540 m (± 446) in winter and 934 m (± 348) in summer (Hayward *et al.* 1993).

Daily Movements

Diurnal Period

Boreal owls move little during the day; they generally remain within the same forest stand during daylight. These owls frequently change roost trees but rarely fly over 40 m when changing roosts (Hayward *et al.* 1993). Based on studies in Idaho (Hayward *et al.* 1993), during daylight boreal owls perch quietly with eyes closed a majority of the time (77% based on 46 hours of observation on 16 days). Periods of sleep rarely exceed 40 minutes and are broken by 2-5 minute periods of preening (6% of time) and looking about (10% of time). Eating (4%), daytime hunting (1%), and moving among roost perches (<1%) are other important daily activities. I observed owls hunt during daylight in winter at 2.9% of roost locations ($n = 448$) and in summer at 7.4% ($n = 446$) of roost locations (Hayward 1989).

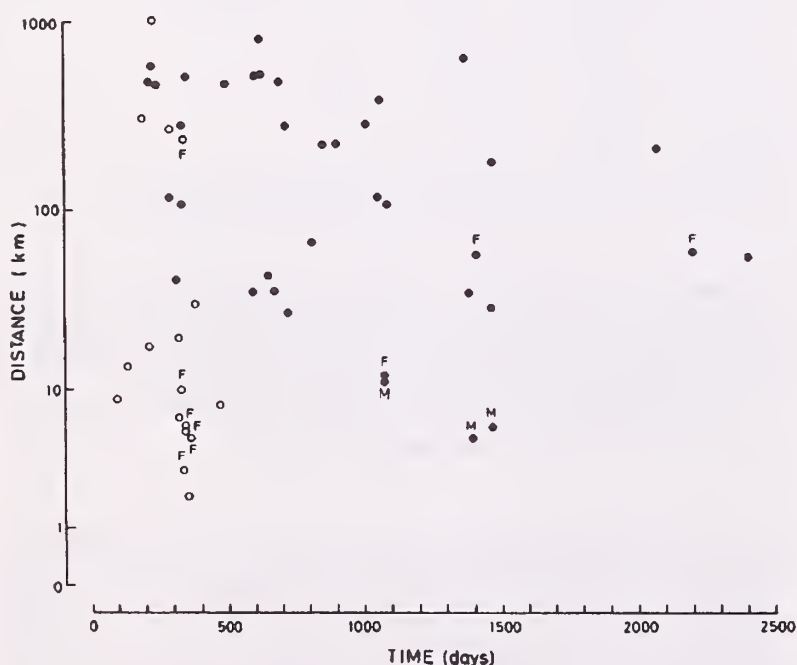


Figure 4.—Distance moved and time elapsed between ringing and recovery of female Tengmalm's owls ringed as nestlings in Norway. Open circles denote dispersals occurring within a microtine peak (high prey availability), while filled circles denote dispersals involving a microtine decline (low prey availability). Males recaptured while breeding are indicated by M, females recaptured while breeding by F (from Sonerud *et al.* 1988).

Nocturnal Period

Nocturnal activity is poorly studied, especially outside the breeding season. Boreal owl foraging activity is concentrated after dark except in northern latitudes during summer. During periods of 24-hour light, foraging is concentrated between sunset and sunrise.

Event recorders have been employed at nest cavities to infer foraging activity patterns of male owls provisioning nests. In Finland, during the incubation period, prey deliveries generally began 1 hour 14 minutes after sunset and ended 49 minutes before sunrise based on records for 6 years (Korpimäki 1981). Depending upon latitude and phase of nesting cycle, night-time activity follows a bimodal pattern with peaks in nest deliveries during the first hours after sunset and again prior to sunrise (Klaus *et al.* 1975, Korpimäki 1981, Hayward 1983). This pattern is most apparent in southern latitudes (i.e., East Germany, Idaho) and early in nesting. In northern Scandinavia, a bimodal pattern appears early in incubation but the two peaks fuse as daylength increases and night-time foraging period decreases (Korpimäki 1981). The foraging activity period also varies depending on phase of the vole cycle. In peak vole years, activity lasted longer each night, the peaks in activity were more pronounced, and prey deliveries after sunrise were more frequent (Korpimäki 1981).

Night-time foraging can be very intense, especially when nestlings near fledging. In Idaho, records from four nests suggest that females leave the nest once each night during incubation (for evacuation) and usually twice after the young hatch (Hayward, G. D. and P. H. Hayward, unpubl. data). Assuming that all records other than for the female's evacuation were prey deliveries, deliveries averaged $3.5 (\pm 0.33 \text{ SD}, n = 84, \text{ range} = 0-9)$ during incubation and $5.0 (\pm 0.61; \text{SD}, n = 6, \text{ range} = 0-12)$ during brooding. Clutches at the four nests were 2, 2, 3, and 3; each fledged two young. In Finland, Korpimäki (1981) estimated 9.8 deliveries/night during brooding period and 8.0 after the female left the nest.

Norberg (1970), Bye *et al.* (1992), and Hayward *et al.* (1993) documented hunting movements of boreal owls. Based on these observations, the owls can be classified as sit-and-wait predators or searchers (as opposed to pursuers) but are very active while hunting. During a foraging bout, the birds move through the forest in an irregular or zigzag pattern, flying short distances between perches (Hayward 1987). They spend a majority of time perched; little time is spent actively pursuing prey. While perched, the owl constantly looks about with rapid head movements,

apparently responding to forest sounds.

When foraging, owls usually fly 10 to 30 m between hunting perches (Norberg 1970, Hayward 1987). In Idaho, over 75% of all flights were 25 m or less. Although the pattern of flights varied, owls observed foraging in Idaho doubled back frequently and, thus, covered a relatively small area within several forest stands rather than a long narrow path. While searching for prey, boreal owls perch on low branches. Perches used during foraging observations in Idaho averaged 4 ± 0.6 m high ($n = 114$). Similarly, average perch height for 17 owls monitored in Norway ranged from 1.7 to 8.7 m (Bye *et al.* 1992).

Boreal owls may traverse several km during a nocturnal foraging bout. Because daytime roosts appear to represent the end of nighttime foraging bouts, locations of consecutive daytime roosts suggest the magnitude of minimum travel distances (Hayward *et al.* 1987b). Distances between consecutive day roosts of 14 owls (7 females and 7 males) on 150 occasions over 4 years in Idaho ranged from 0-6935 m. Mean distances did not differ significantly between winter and summer (winter 1540 [± 446] m, summer 934 [± 348] m). During nesting, five males roosted over 1000 m from their nests 85% of the time (average 1729 [± 831] 200-5600 m) (Hayward *et al.* 1993).

HABITAT USE

Broad Habitat Use Patterns

As year-round residents, boreal owls use similar habitats during all seasons. They occur only in forested landscapes where they nest exclusively in tree cavities or artificial nest structures (Mikkola 1983). The few studies documenting nesting habitat indicate the species uses a range of vegetation types depending on geographic region (e.g., Bondrup-Nielsen 1978, Eckert and Savaloja 1979, Palmer 1986, Korpimäki 1988a, Hayward *et al.* 1993). In northern portions of their range in North America (Alaska and Canada) the owls breed in boreal forest characterized by black and white spruce (*Picea mariana*, *P. glauca*), aspen (*Populus tremuloides*), poplar (*P. balsamea*), birch (*Betula papyrifera*), and balsam fir (*Abies balsamea*) (Bondrup-Nielsen 1978, Meehan and Ritchie 1982). In northern Minnesota and Michigan, singing sites and nests have been documented in old aspen and mixed-forest sites (Eckert and Savaloja 1979, Lane 1988). In the southern portions of their range in North America (Rocky Mountains, Blue Mountains, and Cascades) published research documents boreal owls in subalpine forest habitats characterized largely by subalpine fir (*Abies lasiocarpa*)

and Engelmann spruce (*Picea engelmannii*) and transition forests within 100 m of this elevation (Palmer 1986, Hayward *et al.* 1987a). Because of changes in life zones with latitude, an elevation range cannot be specified for the entire western region of the United States. However, extensive surveys in Idaho and Montana in 1984 and 1985 found no owls below 1,292 m elevation, and 75% of the locations were above 1,584 m (Hayward *et al.* 1987a). Less extensive surveys in northern Colorado found most locations above 3050 m (Palmer 1986).

In USDA Forest Service Regions 1, 2, 4, 6, 9, and 10, biologists have documented boreal owls occurring (but not confirmed breeding) on 26 National Forests and confirmed breeding on 11 other Forests (Chapter 8, table 2). We asked these biologists for an indication of the forest types where boreal owls have occurred. Spruce-fir forest was reported more than any other type (45% of forests with documented breeding). Other forest types in decreasing order of frequency were lodgepole pine (*Pinus contorta*), mixed-conifer, Douglas-fir (*Pseudotsuga menziesii*), aspen (*Populus tremuloides*), black spruce (*Picea mariana*), red-fir (*Abies magnifica*), and western hemlock (*Tsuga heterophylla*).

In Europe, descriptions of breeding habitats have included conifer and deciduous forest types. In Scandinavia, studies report nests in artificial structures hung in pine (*Pinus* spp.), spruce (*Picea* spp.), and birch (*Betula* spp.) forest (Norberg 1964, Korpimäki 1981, Solheim 1983a). In France, "mountain pine" (*Pinus uncinata* and *P. sylvestris*) forest and old forest stands with beech (*Fagus* spp.) were used by owls located by Dejaifve *et al.* (1990:267) and Joneniaux and Durand (1987), respectively. In Germany, conifer forest with old trees were used for nesting (Konig 1969, Jorlitschka 1988).

Landscape Scale Habitat Use

Published accounts of boreal owl habitat use from North America do not directly address patterns of habitat use at the landscape scale. Studies have not compared density, productivity, frequency of breeding attempts, or other measures indexing habitat suitability among landscapes with different mixes of forest cover. Neither have studies directly examined patterns of foraging habitat use across landscapes.

Indirect evidence from Europe and North America does suggest that boreal owls differentiate among forest habitats at the landscape scale. Evidence presented below supports the general statement by König (1969) that "in certain parts of [the study] area

the density of Tengmalm's owls was rather high, while in other ... forests no *Aegolius* existed."

Studies by Hayward *et al.* (1993) in Idaho provide some indirect information on landscape scale habitat use patterns. Nest sites and singing sites (considered representative breeding habitat) were not distributed randomly throughout the study area. Nesting was concentrated in mixed-conifer and aspen forests with no nesting in lodgepole pine forest and infrequent nesting in spruce-fir forests. In contrast, summer roost sites and foraging sites were concentrated in spruce-fir forests. Due to the natural segregation of forest types used for nesting and those used for roosting and foraging, habitat used for different ecological functions was segregated in the landscape. All the resources used by the owls were not provided by any single vegetation type leading to a complex pattern of habitat use. Spruce-fir forest in this study area had few potential nest cavities but small mammal sampling documented that this type supported the most abundant prey populations. In contrast, nest cavities were abundant in mixed conifer forest that supported few prey. Our discussion of microhabitat later provides some insight into landscape patterns through the examination of differences in habitat quality at the stand scale.

Korpimäki (1988a) provides a more direct examination of differences in habitat quality at the landscape scale from his studies in Finland. He rated territory quality of 104 nest sites based on frequency of use over 10 years. Territory occupancy varied from 0 to 9 nestings in 10 years. Poor territories (never occupied) occurred in extensive, uniform forests dominated by pine (*Pinus sylvestris*). These territories had little spruce forest and a high proportion of marshland. The proportion of pine forest decreased and the proportion of spruce forest (*Picea abies*) and agriculture land increased with increasing grade of territories (those with more frequent nesting). The conclusion that territories with spruce forest and agricultural land (in small patches) were the highest quality habitat was corroborated by evidence beyond the frequency of nesting. High quality sites supported breeding during prey crashes, mean clutch size was higher ($P < 0.05$), and number of fledglings was generally greater ($P < 0.05$) than other sites. Poor territories (occupied 0, 1, or 2 times) supported breeding only during peaks in the well-documented vole cycle (Korpimäki 1988a and references therein).

Korpimäki (1988a) explained this pattern based on variation in the abundance and stability of small mammal populations across the vegetation categories.

Spring and fall densities of *Clethrionomys glareolus*, a major small mammal prey, were three times higher in spruce than pine forests (Korpimäki 1981). The mean densities of small birds, important alternative prey, were also higher in spruce forests than in pine (331 versus 260 pairs/km²) (Korpimäki 1981). Furthermore, small mammal populations were more stable in the spruce forests than other types (Korpimäki 1988a). Korpimäki (1988a) pointed out that the pattern of habitat occupancy (virtually all habitats used in vole peaks but only "good" territories occupied during cyclic lows) fit the Fretwell and Lucas (1969) "ideal free" model of habitat use. Thus the size of the breeding population strongly influenced the pattern of habitat use at the landscape scale.

Home Range Scale Habitat Use

Home range size and movements within boreal owl home ranges was discussed in the Movements Within the Home Range section. Research in North America has not directly examined patterns of habitat use within individual home ranges except at the microhabitat scale which is discussed below. Patricia Hayward and I are currently analyzing data collected during the study reported in Hayward *et al.* (1993) at the home range scale but results are not yet available.

Sonerud *et al.* (1986) provide some data at this scale based on observations of a single radio-marked male owl followed on five nights. Because the results stem from observations of a single bird during a single week, general patterns cannot be inferred. The results are important, however, because they are the only data currently available and the pattern observed corroborates results reported throughout this section. The owl used an area of 205 ha during the 5 nights (based on 107 nocturnal locations using a minimum convex polygon estimator). Nightly use areas ranged from 40-78 ha and the maximum distance between foraging areas and the nest for each night varied from 1030-1320 m. While foraging, the owl favored old forest and avoided clear cuts and young plantations in spite of lower prey densities in the former (Sonerud *et al.* 1986:105).

Microhabitat

Nest Sites

A majority of nest site locations described in the literature have not resulted from efforts designed to survey a range of habitats to determine both habitats used and those not used. The results, then, can-

not be interpreted as an indication of selection but rather to describe some subset of used habitats. In Alaska, eight nests located near Fairbanks occurred in closed-canopy deciduous or mixed forest; none occurred in uniform conifer forest (Meehan and Ritchie 1982). Of five nests in natural cavities, four occupied flicker holes and one a natural cavity. In Canada, Bondrup-Nielsen (1978) located 6 nests, all in aspen—3 in live trees, 3 in snags. Minnesota nests have been documented in old aspen clones intermixed with conifers (Eckert and Savaloja 1979 and Lane 1988). In a more extensive investigation involving 9 National Forests in Montana and Idaho, 76% of 49 boreal calling sites (recognized as potential breeding sites) occurred in mature and older forest stands (Hayward *et al.* 1993). The exceptions were locations in lodgepole pine (*Pinus contorta*) stands in drainages where lodgepole was the only forest type. The majority (88% of 49 observations) of owls were located in stands on subalpine-fir habitat types. Proportions for other habitat types included Engelmann spruce (3%), Douglas-fir (6%), and western hemlock (3%).

During 4 years of study in the wilderness of central Idaho, Hayward *et al.* (1993) documented nests in stands of old mixed-conifer (11), old Engelmann spruce (7), old aspen (5), and old Douglas-fir (5) forest. A nest box experiment in the same area suggested that owls avoided nesting in forests lacking the structural features of mature and old forest when alternate sites in old forest were available (Hayward *et al.* 1993). This study did examine available forest structure and compared used sites with a sample of available sites. Forest structure at nest sites differed from the random sample (101 sites) of available forest. Used sites occurred in more complex forest, with higher basal area, more large trees, and less understory development than available sites. The forest immediately around nest trees had an open structure. Density of trees 2.5 to 23-cm-dbh (diameter at breast height) in a 0.01-ha plot around the nest tree averaged 398 ± 162 /ha (range 0-1,482). The density of trees at nests was three times lower than the average at winter roost sites. Nest sites averaged $57 (\pm 16)$ trees/ha over 38 cm dbh, $17.8 (\pm 3.1)$ m²/ha basal area, and 30% (± 4.3) overstory (> 8 m above ground) canopy cover (this is not total canopy cover but cover of upper canopy). Stands used for nesting supported an average of $9 (\pm 6.0)$ snags per ha over 38 cm dbh. Size of the stand containing the nest ranged from 0.8-1.3 ha in aspen and 1.6-14 ha in conifer forest.

The range of sites used by boreal owls is quite broad despite the evidence that the species chooses particular forest structures when a variety of nest

sites are available. In Idaho and Norway nest boxes in clearcuts have been used (see Sonerud 1989 and Hayward *et al.* 1992). The use of these sites, however, does not indicate that this is high quality habitat.

Nest Tree and Cavity Characteristics

Boreal owls are secondary cavity nesters and nest primarily in cavities excavated by pileated woodpecker (*Dryocopus pileatus*) and northern flicker (*Colaptes auratus*) in North America, and black woodpecker (*Dryocopus martius*) cavities or nest boxes in Europe. In central Idaho 18 of 19 nests were attributed to pileated woodpeckers; a northern flicker probably excavated the other. Cavity dimensions averaged 31 cm (± 7.61 ; $n=19$, range 7-50) deep and 9 cm (± 2.11 range 15-26) horizontally. Cavity entrances measured 102 mm (± 12.41 range 64-150) high and 95 mm (± 11.89 range 56-148) wide (Hayward *et al.* 1993).

Nests located in Idaho were generally in large trees or snags. Tree diameter at the cavity averaged 41 ± 5.21 cm (range 26-61 cm) and tree dbh averaged 64 ± 11.02 cm (range 33-112 cm). The smallest of these were all aspen and, therefore, still larger trees grew in the nest stand. Ten (of 19) nests occupied snags, including eight ponderosa pine, one aspen, and one Douglas-fir. Snag condition included 3 old branchless snags >11 m tall, 2 hard snags with sloughing bark and only large branches remaining, and 5 young snags with bark and complete limbs (Hayward *et al.* 1993).

In contrast with nest conditions in the United States, over 90% of some Scandinavian populations nest in artificial structures. This pattern is attributed to the scarcity of primary cavity nesters and paucity of large old trees (Korpimäki 1981, 1985).

Roost Sites

Three studies in North America addressed roosting habitat: one in Canada by Bondrup-Nielsen (1978), one in Colorado by Palmer (1986), and one in Idaho by Hayward and Garton (1984) and Hayward *et al.* (1993). These studies demonstrate that, unlike many forest owls, individual boreal owls roost at many different sites and choose roosts dispersed widely throughout their home range. The available evidence suggests that under some circumstances (see below) the owls select particular forest conditions for roosting but much of the time are unselective.

In Canada, 30% of 30 roosts located in spring and summer were in aspen or birch; the remainder were in conifers (Bondrup-Nielsen 1978). Based on com-

parison with paired random sites, Bondrup-Nielsen (1978) concluded that the owls were not selective in roost choice. In Colorado, 174 roosts located in winter and summer did not differ significantly between seasons although low statistical power may have led to this conclusion. It was not clear from the analysis whether forest structure at roosts differed from paired random sites. Combining seasons, roost sites averaged 14.7 trees/ha >39 cm dbh, 6 snags/ha, and 44% canopy cover (Palmer 1986). Average species composition of roost stands were 42% Engelmann spruce, 42% subalpine fir, and 6% lodgepole pine suggesting that the owls choose late successional stands for roosting.

In Idaho, based on habitat measurements from 430 roosts used by 24 radio-marked owls, habitat type (as defined by Steele *et al.* 1981) and forest structure differed between roosts used in winter and summer ($P < 0.001$, Hayward *et al.* 1993). Forest stands used for winter roosts averaged 58% canopy cover, 26 m²/ha basal area, 1,620 trees/ha with 2.5-23 cm dbh, and 165 trees/ha over 23.1 cm dbh. Summer roosts averaged 63% canopy cover, 30 m²/ha basal area, 2,618 trees/ha with 2.5-23 cm dbh, and 208 trees/ha over 23.1 cm dbh. Winter and summer roosts differed in all aspects of forest structure measured. All roosts ($n=882$) were in conifers; the owls were never observed roosting in cavities as is reported in Europe (Korpimäki 1981).

In the same study, roost sites were compared with paired random sites using a paired Hotelling's T^2 (189 winter, 241 summer sites). The results provided strong evidence for selection in summer, but results for winter also suggested selection (winter $P = 0.021$; summer $P < 0.0001$). Summer roosts occurred at cool microsites with higher canopy cover, higher basal area, and greater tree density than paired random sites (Hayward *et al.* 1993). When the authors compared temperature at the roost and in the nearest opening (both temperatures taken in the shade while the owl was roosting), roost sites were significantly cooler when ambient temperatures exceeded 4° C ($P < 0.001$). The difference in temperature increased with increasing ambient temperature and the owls gular fluttered when temperatures were as mild as 20° C. The authors concluded that in summer, the owls chose cool microsites for roosting to avoid heat stress. In winter, the owls did not appear to be thermally stressed and used a wider variety of roost conditions.

Foraging Sites

The nocturnal foraging pattern of boreal owls has hampered attempts to study foraging habitat use

(Hayward 1987). Therefore, the inferences concerning foraging habitat are largely based on indirect evidence.

Studies in Idaho (Hayward 1987, Hayward *et al.* 1993) based on roost locations (assumed to represent the end of a foraging bout) suggest that mature and older spruce-fir forests were important for foraging. Owls were observed successfully foraging in these forests and the locations of radio-tagged birds also indicated male owls were hunting in these forests while feeding young at nests located at lower elevations. Data on prey distribution and food habits further supported this contention (Hayward *et al.* 1993). Palmer's (1986) observations in Colorado also indicated older spruce-fir forest was used for hunting.

Studies in Norway also noted the importance of mature spruce forest for foraging (Sonerud 1986, Sonerud *et al.* 1986). Direct observations and diet indicated that during winter and summer the owls foraged primarily in older forest sites. In early spring, immediately following snowmelt, owls hunted clearcuts for a short period until lush vegetation developed. Owls favored mature forest during winter because snow conditions (uncrusted snow) facilitated access to prey. In summer, mature forest sites had less herbaceous cover than open sites that allowed greater access to prey. Following spring thaw, before herbaceous vegetation became dense, owls shifted to openings where densities of voles exceeded densities in forested stands.

In his 1987 address to the Northern Owl Symposium, Norberg (1987) highlighted the morphological adaptations of *Aegolius funereus* that facilitate foraging in forest stands at night. He noted the extreme skeletal asymmetry that facilitates ocular prey detection and localization under dark forest conditions. The short, broad, rounded wings of the boreal owl facilitate silent, agile flight in tight forest conditions. These morphological characteristics open up possibilities for exploiting habitat types unavailable to species lacking the traits. He also noted that the light wing-loading of boreal owls allow individuals to efficiently forage among habitat patches dispersed throughout their home ranges without expending excessive energy commuting between patches. Furthermore, the light wing-loading reduces the cost of foraging at distant sites and transporting prey back to the nest. This line of reasoning corroborates the limited observations that suggest that small, dispersed patches of high quality foraging habitat (high prey availability) are hunted by boreal owls who use large home ranges.

Morphology, of course, is not the only potential explanation for observed habitat use patterns. Predators and competitors may also influence foraging habitat use.

FOOD HABITS

Feeding

Foraging Movements

Boreal owls hunt primarily after dark except in northern regions without summer darkness (Norberg 1970, Mikkola 1983). In southern areas the species exhibits a biphasic rhythm with peaks of activity 2000-2200 h and 0200-0500 h (Mikkola 1983). Prey deliveries at monitored nests in Idaho (Hayward, G. D. and P. H. Hayward, unpubl. data) never occurred between sunrise and sunset; however, owls observed on daytime roosts ($n = 882$) occasionally hunted in daylight (13 observations in winter, 33 observations in summer) (Hayward *et al.* 1993). On 10 occasions the author observed owls capture prey from daytime roosts.

Boreal owls forage using sit and wait tactics (as opposed to pursuit). Four owls observed foraging on 13 occasions in Idaho moved through the forest in a zig-zag pattern, flying short distances ($\bar{x} = 25 \pm 8$ m; $n = 123$) between perches. Perch heights averaged $4 (\pm 0.6 \text{ } n = 114)$ m, and owls watched for prey for less than 5 minutes on 75% of 150 perches (Hayward *et al.* 1993). Norberg (1970) recorded perch heights averaging 1.7 (0.5-8) m ($n = 154$) and flight distances of 17 (2-128) m, and Bye *et al.* (1992) recorded similar observations.

Prey Capture

Boreal owls observed in Idaho usually attacked prey within 10 m of their hunting perch (Hayward *et al.* 1993). In Norway, Bye *et al.* (1992) reported attack distances (direct distance between the owl and the prey) from 2.2 to 12.6 m. Successful attacks averaged 5.3 m ($n = 10$) and unsuccessful attacks 6.1 m ($n = 10$). Norberg (1970) describes pouncing and killing behaviors in detail. He (Norberg 1970, 1987) notes observations of boreal owls capturing prey either under the snow surface (plunge diving) or obscured by vegetation. The ability to locate prey aurally is attributed to the extreme asymmetry of the owl's skull (Norberg 1978, 1987), which permits localization of sounds in vertical, as well as horizontal, directions.

Diet

In North America, usual prey species are voles, particularly red-back voles (*Clethrionomys gapperi*), heather voles (*Phenacomys intermedius*), northern bog lemming (*Synaptomys borealis*), and *Microtus* spp.; mice, including deer mice (*Peromyscus* spp.) and jumping mice (*Zapus princeps*); shrews, (*Sorex* spp.); northern pocket gophers (*Thomomys talpoides*); squirrels, including northern flying squirrels (*Glaucomys sabrinus*) and chipmunks (*Tamias* spp.); birds, especially thrushes (*Catharus* spp.), warblers, dark-eyed junco (*Junco hyemalis*), red crossbill (*Loxia curvirostra*), American robin (*Turdus migratorius*), mountain chickadee (*Parus gambeli*), common redpoll (*Carduelis flammeus*), kinglets, and woodpeckers; and insects, especially crickets (Bondrup-Nielsen 1978, Palmer 1986, Hayward and Garton 1988, Hayward *et al.* 1993). Weasel (*Mustela* spp.), woodrat (*Neotoma cinerea*), juvenile snowshoe hare (*Lepus americanus*), and pika (*Ochotona princeps*) represent unusual prey.

Within North America, little difference in diet is apparent between studies in Alaska (T. Swem, pers. comm.), Canada (Bondrup-Nielsen 1978), and the Rocky Mountains (Palmer 1986, Hayward *et al.* 1993). In each locale, red-backed voles (*Clethrionomys* spp.) and *Microtus* spp. were dominant prey.

Boreal owl food habits have been studied more thoroughly in Europe; for a summary see Cramp (1977). The results are surprisingly similar to North America. *Clethrionomys* sp. and *Microtus* sp. dominate the diet in most cases. Results suggest, however, that in Scandinavia, boreal owls consume more voles associated with open habitats than are recorded in the Rocky Mountains of North America. This could be due to differences in habitat characteristics in particular study areas, in the owls foraging behavior, in predation risks, or in competitive interactions.

Quantitative Analysis

Most samples of boreal owl prey in North America are small. Bondrup-Nielsen (1978) reported 58 individual prey from his two study sites in Canada, Palmer (1986) recorded 72 prey found in 4 years in Colorado, and Hayward *et al.* (1993) reported 914 prey identified from 4 years in Idaho (table 1). These data are not sufficient to make in-depth comparisons between geographic areas, examine functional or numeric responses to changes in prey populations, or predict changes in diet or owl demography in response to changes in prey populations. As a group, however, these investigations cover a broad geographic area and provide a sound basis for gen-

eralizations concerning boreal owl diet in North America.

The breadth of prey represented in the boreal owl diet contrasts with the narrow range of prey taken frequently. The data suggest that the boreal owls are vole specialists under most circumstances. *Microtus* and *Clethrionomys* constituted 45 and 31% (by frequency) of prey identified from the two study sites in Canada (Bondrup-Nielsen 1978). In Colorado, *Clethrionomys* and *Microtus* were 54 and 25% of the diet (Palmer 1986). In Idaho, red-backed voles were

the most frequent prey in summer (35% by frequency) and winter (49% by frequency) (32 owls over 4 years). In terms of prey biomass, red-backed voles accounted for 37% of the annual prey. Northern pocket gophers (26%) and *Microtus* spp. (11%) were the only other species accounting for over 10% of the annual prey biomass (Hayward *et al.* 1993). Northern flying squirrels were captured by female owls in winter and accounted for 45% of winter prey biomass. Overall, small mammals accounted for 79% of prey (95% of estimated biomass).

Table 1. – Diet of boreal owls in Idaho (Hayward *et al.* 1993), Colorado (Palmer 1986), and Canada (Bondrup-Nielsen 1978) based on pellets and prey identified from nests.

Prey	Idaho		Colorado	Canada
	% of prey items	Biomass ¹ (%)	% of prey items	% of prey items
Mammals				
Red-backed vole (<i>Clethrionomys</i> spp.)	36	37	54.2	31
Northern pocket gopher (<i>Thomomys talpoides</i>)	10	26		
Unidentified shrews (<i>Sorex</i> spp.)	11	3	5.5	2
Unidentified voles (<i>Microtus</i> spp.)	9	11	25	45
Deer mouse (<i>Peromyscus maniculatus</i>)	6	5	1.4	10
Heather vole (<i>Phenacomys intermedius</i>)	4	3		
Northern flying squirrel (<i>Glaucomys sabrinus</i>)	1	7		
Chipmunk (<i>Tamias</i> spp.)	2	3	1.4	
Jumping mouse (<i>Zapus princeps</i>)	2	1		
Woodland jumping mouse (<i>Napaeozapus insignis</i>)				3
Pica (<i>Ochotona princeps</i>)	tr ²	tr		
Woodrat (<i>Neotoma cinerea</i>)	tr	tr		
Unidentified weasel (<i>Mustela</i> spp.)	tr	tr		
Water vole (<i>Microtus richardsoni</i>)	tr	tr		
Birds	5	3	7	5
Insects	13	1		
Total count	914	-	72	58

¹ Biomass calculated using values from Hayward *et al.* (1993).

² tr indicates <1%.

Quantitative results from Europe demonstrate a similar pattern. *Microtus* and *Clethrionomys* dominate the diet in most locales but a more varied diet is evident in more southern populations (Korpimäki 1986b). In an 8 year study documenting contents of 67 owl nests in central Finland, Jäderholm (1987) found *Clethrionomys* spp. and *Microtus agrestis* together accounted for 80% of Tengmalm's owl prey biomass. Shrews were the next most important prey, accounting for 18% of individual prey and 8% of the biomass. Korpimäki's (1986c, 1988b, Korpimäki and Norrdahl 1989) work in western Finland reveals a similar pattern. *Microtus* spp. were the most abundant prey in nests (45% by frequency), followed by *Clethrionomys* spp. (32%), shrews (15%), and birds (5%). Values for prey identified from pellets differed in that shrews dominated the sample (33% by frequency), followed by *Microtus* spp. (27%), *Clethrionomys* spp. (24%), and birds (12%).

In Czechoslovakia, mice (especially *Apodemus* spp. and *Muscardinus avellanarius*, together 18% of prey biomass) were more important in the diet than in more northern populations and the diet included more species of mammals (24 species) (Kloubec and Vacík 1990). *Microtus* spp., *Sorex* spp., and *Clethrionomys* spp. were still major prey, together accounting for 39% of prey biomass. This study summarized information from 11 sites distributed throughout Czechoslovakia. Schelper (1989) summarized information from another southern population, in Germany. *Apodemus* spp. dominated the prey (39%) followed by *Microtus* spp. (25%), *Clethrionomys* spp. (14%), *Sorex* spp. (12%), and birds (6%).

Marti *et al.* (1993) summarized results of 20 papers from Europe and 4 from North America and found the geometric mean weight of prey for 4 regions in Europe, moving northward, to be 14.7, 17.6, 15.0, and 19.9 g; and 19.2 and 22.2 g for the Rocky Mountains and Alaska, respectively. In Europe, food-niche breadth declined from southern to northern populations while in North America food-niche expanded in northern populations (Marti *et al.* 1993).

Seasonal Variation

Boreal owl diets differ from winter to summer due to the natural variation in availability of prey due to snow cover and the hibernation of some small mammal prey. In Idaho, northern pocket gophers (one of the most frequent summer prey), western jumping mice, and yellow-pine chipmunks were all unavailable in winter. The owls relied on southern red-backed voles for nearly 50% of winter prey. Flying squirrels were captured far more frequently in winter than summer. Of 12 recorded flying squirrel prey,

11 were captured during winter, 10 of these by females. The squirrels represented 45% of prey biomass recorded for female owls during winter, indicating the importance of these prey when other prey are less available. During summer, southern red-backed voles continued to be the most frequent prey and accounted for 31% of prey individuals. The owl summer diet was diverse compared to winter with the addition of chipmunks, jumping mice, and crickets. The relative importance of birds in the diet did not change between seasons (5% by frequency).

In Finland, the owl's diet shows a marked seasonal pattern that varies depending on the stage of the multi-year vole cycle (tables 2 and 3). This study covered the period January-June from 1973-1985 and included four peak vole phases. In all years, birds were important from January through mid-March (24-24% of diet by frequency) and in late May and June (8 - 27%) while shrews increased in the diet as they matured in late April. In good vole years, *Microtus* spp. were taken most frequently in late March and April (74-84% of diet) and formed 35-49% of the diet in other months. During the high vole years, *Clethrionomys* captures increased in late April as *Microtus* became less important. In poor vole years the frequency of *Clethrionomys* in the diet increased earlier in March, when they accounted for 51% of the diet; *Clethrionomys* captures remained high through May.

Yearly Variation

In Idaho, *Clethrionomys gapperi* varied from 26 to 45% of the annual diet (by frequency) over 4 years (Hayward *et al.* 1993). Deer mice, pocket gophers, and heather voles (*Phenacomys intermedius*) increased in years when *Clethrionomys* was less frequent. Years with a low proportion of *Clethrionomys* were poor breeding years for the owl. The frequency of *Microtus* spp. remained relatively constant during this study and averaged 11%. The frequency of shrews and birds also remained relatively constant.

In Finland, the owl's diet varied sharply among years in response to the well documented (e.g., Hansson and Henttonen 1985) vole cycle (Korpimäki 1988b). The proportion of *Microtus* in diet correlated positively (Spearman rank correlation: $r_s = 0.86$, $P < 0.001$) with the abundance of these voles in spring trapping samples and varied from 6 to 71% of the diet (Korpimäki 1988b). Proportions of shrews and birds in the diet varied inversely with the numbers of *Microtus*. The proportion of *Clethrionomys* in the diet correlated positively with the proportion of *Microtus* ($r_s = 0.46$, $P < 0.10$) and varied from 3 to 45% of prey.

Table 2.—The seasonal changes in the food composition (as percentages by number) of the Tengmalm's owl during the first half of the year in peak vole years (pooled data from 1973, 1977, 1982, and 1985). The statistical significance of the differences between consecutive time periods was examined using chi-square tests. From Korpimäki (1986c).

Prey groups	Time periods							Total
	1 Jan.-15 March	16-31 March	1-15 April	16-30 April	1-15 May	16-31 May	1-30 June	
Shrews	17.3	2.4	4.6	15.9	10.5	15.8	20.0	11.8
Water vole	-	-	-	-	0.2	-	-	0.1
Bank vole	17.3	11.2	15.5	34.0	34.1	27.2	20.0	27.7
<i>Microtus</i> spp.	34.7	84.0	74.0	46.6	49.0	45.1	48.0	52.4
Murids	6.7	2.4	5.5	2.8	5.6	-	-	4.1
Birds, adults	24.0	-	0.5	0.7	0.7	12.0	8.0	3.9
nestlings and young		-	-	-	-	-	4.0	0.1
total birds	24.0	-	0.5	0.7	0.7	12.0	12.0	4.0
No. of prey items	150	125	219	427	602	184	25	1732
Diet width	9.04	2.49	3.12	4.02	3.98	5.15	4.25	
χ^2	45.80	26.38	65.39	13.64	54.80	5.49		
df	4	4	5	5	5	4		
$P <$	0.001	0.001	0.001	0.05	0.001	ns		

Table 3.—The seasonal changes in the food composition (as percentages by number) of the Tengmalm's owl during the first half of the year when vole populations were not at a peak (pooled data from 1974-76, 1978-81, and 1983-84). Statistical analysis same as in table 1. From Korpimäki (1986c).

Prey groups	1 Jan.-15 March	16 March- 15 April	16-30 April	1-15 May	16-31 May	1-30 June	Total
Shrews	11.9	17.1	26.0	24.0	36.8	45.8	25.2
Red squirrel	-	0.3	-	-	-	-	0.0
Water vole	-	0.3	0.3	0.2	-	0.6	0.2
Bank vole	9.9	51.6	46.5	42.3	19.6	14.5	35.4
<i>Microtus</i> spp.	42.9	25.1	23.1	18.8	7.7	4.2	21.8
Murids	1.4	4.8	3.2	3.6	4.2	-	3.2
Birds, adults	34.0	0.9	1.0	11.2	26.7	18.7	12.3
nestlings and young	-	-	-	-	4.9	16.3	1.9
total birds	34.0	0.9	1.0	11.2	31.6	34.9	14.2
No. of prey items	294	351	624	421	285	166	2141
Diet width	8.18	3.05	3.24	3.95	5.20	4.13	
χ^2	222.10	9.02	50.47	84.56	6.28		
df	5	5	5	5	4		
$P <$	0.001	0.10	0.001	0.001	ns		

Energetics

During the nestling period, young owls in Finland consume an average of 21 g per bird per day and captive adults 65 g/day (Korpimäki 1981). Jäderholm (1987) calculated that during nesting, young boreal owls are provided about 650 g of prey,

which is similar to Korpimäki's estimate for a 29-30 day nestling period. Prey biomass provided for each nestling changed little for broods from 2-7 nestlings but was higher when only one nestling was present (about 1,600 g) (Jäderholm 1987:Fig 3).

As an indirect measure of prey consumed in Idaho, Patricia Hayward and I monitored four nests with

mechanical event recorders triggered by a perch mounted at the cavity. These records suggested that the female left the nest once each night during incubation (for gut clearing) and usually twice after the young had hatched. Assuming that all records other than female gut clearing were prey deliveries, deliveries averaged 3.5 (± 0.33 ; $n = 84$ nights of records; range 0-9) during incubation and 5.0 (± 0.61 ; $n = 76$ nights; range 0-12) during brooding. Clutches at the four nests were 2, 2, 3, and 3; each fledged two young. Korpimäki (1981) estimated 9.8 deliveries/night during brooding period and 8.0 after the female left the nest.

Temperature Regulation

No data have been published on thermal neutral zone, basal metabolic rate, and metabolism while active. Winter and summer roost characteristics indicate boreal owls in central Idaho were not stressed by winter conditions but chose roosts to reduce summer heat stress (Hayward *et al.* 1993). Guller fluttering was noted only in summer but occurred when temperatures at roosts were as mild as 18°C and 23°C, suggesting the owls are easily heat stressed.

Food Caches

Immediately prior to nesting (1-2 weeks) and during nesting, prey are cached in the nest cavities (Norberg 1987). In Finland (13-year study, Korpimäki 1987a), the size of nest caches was related to phase of the vole cycle. During peak phase, caches averaged 6.9 items/nest weighing 89.3 g; in low phase, 1.5 items/nest weighing 19.6 g. *Clethrionomys glareolus* were the most common cached prey. Prey are also cached at roosts. In Idaho, owls were observed retrieving cached prey or caches were observed near roosting owls at 17% of summer and 4% of winter roost locations ($n = 882$).

ECOLOGY OF PRINCIPAL PREY

Forest dwelling small mammals dominate boreal owl diets in most regions (see previous Food Habits section). In North America, important species include red-backed voles, flying squirrels, deer mice, shrews, and pocket gophers. Microtine voles are also important throughout the species' range and seem to increase in importance in more northern latitudes. In this section I will briefly review the ecology of several prey species that occurred frequently in boreal owl diets in the United States: red-backed vole, deer mouse, flying squirrel, and other voles (Palmer

1986, Hayward *et al.* 1993). This review is intended only to give the reader a preliminary understanding of small mammal prey as a background for the remainder of the conservation assessment. I concentrate on habitat use and food habits of the selected prey species.

Red-Backed Vole

The genus *Clethrionomys*, or red-backed voles, occurs throughout the range of boreal owls and represents an important prey genus in all populations studied. These 20-30 g voles are active year-round and their circadian activity pattern includes periods of foraging throughout the 24 hour cycle (Stebbins 1984). Red-backed voles do not form colonies but nest singly or in family groups in natural cavities, abandoned holes, or nests of other small mammals near the ground surface. During winter they spend most of their time at the snow-ground interface.

The genus occurs almost exclusively in forest habitats although Whitney and Feist (1984) describe populations occurring in grassland habitats in Alaska. Merritt (1981:4) characterizes their habitat as "chiefly mesic habitats in coniferous, deciduous, and mixed forests with abundant litter of stumps, rotting logs, and exposed roots." In Idaho, red-backed voles were most abundant in mature and older spruce-fir forest where they were the most abundant small mammal (Hayward *et al.* 1993). The relationship between forest successional stage and red-backed vole abundance appears to vary geographically. In the western and northeastern portions of North America, red-backed voles are most abundant in mesic, mature conifer forest, particularly spruce-fir forests (Brown 1967, Scrivner and Smith 1984, Millar *et al.* 1985, Raphael 1988). In these regions red-backed voles decline sharply after clearcutting (Campbell and Clark 1980, Ramirez and Hornocker 1981, Halvorson 1982, Martell 1983a, Medin 1986). Martell (1983b) showed that the loss of red-backed voles from clearcuts may lag 2-3 years, but the voles were still rare after 13 years. In contrast to the radical population changes observed after clearcutting, red-backed vole populations remained abundant after patch cutting (3 acre clearcuts) and selection harvest in several locales (Campbell and Clark 1980, Ramirez and Hornocker 1981, Scott *et al.* 1982, Martell 1983b). Wywiałowski (1985), using voles caught in Utah and placed in an artificial experimental arena, showed that the voles preferred areas with greater overstory cover.

Observations in the central and southeastern portion of the species' range suggest a more varied pat-

tern of habitat use (see references in Merritt 1981). In Minnesota, Michigan, Maine, and Nova Scotia red-backed voles were common, or in some cases, most abundant in clearcut sites or sapling stages following cutting (Swan *et al.* 1984, Probst and Rakstad 1987, Clough 1987). The pattern seems to be associated with moist deciduous forests where sites remain mesic after deforestation.

Food habits of red-backed voles fit their association with forest habitats. Hypogeous ectomycorrhizal and surface fruiting fungi are dominant foods in many regions (see references in Merritt 1981 and Ure and Maser 1982). These fungi are associated with tree roots, rotting logs, and litter on the forest floor in mesic forest stands. Fruticose lichen, particularly the arboreal *Bryoria* spp., are important food across the species' range, especially in winter (Martell and Macaulay 1981, Ure and Maser 1982). In Ontario, lichen and fungi together formed 80-89% of the diet across four study sites (Martell and Macaulay 1981). Ure and Maser (1982) noted that lichen is especially important to voles at higher elevations where the fruiting season for fungi is brief. Other foods include green vegetation (e.g. leaves of *Vaccinium* spp.), seeds, berries, and some insects in summer and autumn.

Non-Forest Voles

Voles in the genus *Microtus* are consumed by boreal owls throughout the owl's range in North America (table 1). Predation on *Microtus* is especially significant because these 25-40 g rodents occur most commonly in nonforested habitats. *Microtus* are active year round; they nest on the ground surface in grass nests and live at the snow-ground interface during winter. *Microtus* feed almost exclusively on leafy vegetation and the inner bark of small trees and shrubs (Vaughan 1974). Numerous studies demonstrate that, aside from dispersing individuals, these voles do not occur in forest stands (see references in Johnson and Johnson 1983). Populations will occur in small (several acres) grassland or shrub openings in otherwise forested landscapes.

Deer Mouse

Deer mice (*Peromyscus* spp.) are eaten frequently by boreal owls throughout North America but never are the dominant prey. These 20-30 g mice are highly nocturnal (Stebbins 1984) and active year-round. Deer mice are partially arboreal (Getz and Ginsberg 1968). Their diet is omnivorous, being dominated by seeds (Martell and Macaulay 1981). Compared

with other small rodents their population densities are relatively stable (Van Horne 1982).

Deer mice occupy both forested and open habitats from desert to temperate rain forest. Within the geographic range and life zone used by boreal owls, deer mice occupy most habitats. In the mountains of Colorado deer mice were captured in a wider variety of montane habitats than other rodents (Williams 1955). In Idaho, deer mice were captured in spruce-fir forests, Douglas-fir forests, lodgepole pine forests, ponderosa pine forests, and sagebrush-bunchgrass openings. Wet meadows were the only habitats where the mice did not occur (Hayward *et al.* 1993). In most locales these mice increase or remain equally abundant with disturbance or deforestation (Campbell and Clark 1980, Ramirez and Hornocker 1981, Van Horne 1981, Halvorson 1982, Martell 1983a, Buckner and Shure 1985, Medin 1986). Deer mice tend to be more abundant than red-backed voles in drier, rockier, forested habitats that are dominated by pines rather than spruce or firs (Millar *et al.* 1985, Raphael 1988).

Northern Flying Squirrel

Northern flying squirrels have been identified as important prey in only a single study in North America (Hayward *et al.* 1993); however, in this study, northern flying squirrels represented 45% of the prey biomass for female owls during winter. These ~140 g squirrels are highly nocturnal and active year-round (Wells-Gosling and Heaney 1984). Their diet is poorly understood, but fungi and lichens are thought to be the major foods in areas without substantial mast crops. Other foods include buds, catkins, fruits, tree sap, and insects (Wells-Gosling and Heaney 1984). Lichen is also important to the squirrels as a winter nesting material (Hayward and Rosentretter 1994). As with diet, habitat relationships are poorly understood. Across their extensive range, northern flying squirrels are found in conifer, hardwood, and mixed forests (Wells-Gosling and Heaney 1984). Squirrel densities in Douglas-fir forests of the Oregon Cascade Range were not correlated with habitat characteristics (Rosenberg and Anthony 1992). The only substantial published study linking flying squirrels with older forest has been questioned (see Rosenberg *et al.* in press concerning Carey *et al.* 1992). It is therefore interesting that mature and older forests provide necessary foods such as fungi, lichen, and large mast crops that do not occur commonly in younger forests.

BREEDING BIOLOGY

Phenology of Courtship and Breeding

Data on the phenology of courtship and breeding for populations in North America stem from a handful of studies that were not designed to address this topic *per se*.

Courtship

In Colorado, singing began by mid-February, early March, late March, and mid-April in 4 years. Courtship singing by individual owls lasted up to 102 days with an average of 26 (4-59, $n = 4$) days for successful males (Palmer 1986). In Idaho, during 3 good breeding years, males were heard on 27 January, 30 January, and 16 February (each within 2 days of beginning field-work). During a poor breeding year, calling was first heard 9 February, 16 days after field-work was begun. At a similar latitude in Europe (Germany), singing begins around the first of January (Schelper 1989). In Sweden, Carlsson (1991) found individual males began singing on some successful territories over 2 months after the first males began singing. Late singers tended to be younger and may have immigrated into the area. Daylength, prey availability, and nightly minimum temperatures (Bondrup-Nielsen 1978, Korpimaki 1981) are purported to determine onset of the courtship period. The variation observed in courtship activity suggests that prey availability, weather conditions, and resident status interact to modify the influence of daylength, which likely acts as the primary factor.

During courtship, displays are limited to flights by the male between perches near the female and a potential nest cavity, accompanied by vocalization of the "prolonged song" or extended singing from the nest cavity. Courtship feeding may begin 1-3 months prior to nesting. The female occupies the nest up to 19 days and usually 1 week prior to laying (Hayward 1989) and is fed nightly by the male.

Nest Occupancy

Courting owls rendezvous nightly at the potential nest site toward the end of the courtship period where the male displays and presents food. Late in the courtship season, prior to laying, the female occupies the cavity day and night for 1-19 (usually ~6) days where she is fed by her mate. Over 4 years, known first day of occupancy ranged from 13-30 April for seven owls in Idaho (Hayward 1989).

Egg Laying

In Minnesota, clutches were initiated by 30 March and 12 April (Lane 1988). In Colorado, laying dates were estimated from 17 April to 1 June with half the known nests being initiated by 10 May (R. Ryder, Colo. State Univ., Ft Collins Co). In the central Idaho wilderness, initiation dates extended from 12 April to 24 May with half the nests begun by 1 May (5 years, 13 nests; Hayward 1989). Near Anchorage, Alaska, nests located in nest boxes were initiated from 27 March to 5 May with a median date of 10 April (T. Swem, U.S. Fish & Wildl. Serv., Fairbanks, AK). A population in Germany began laying as early as February in good vole years but more often in April (Schelper 1989). Finnish nests were initiated from 8 March to 15 May with over half begun before 10 April; nests were initiated earlier in good prey years (12 years; Korpimaki 1981). Studies in Norway suggest that second clutches of biandrous females were laid 50-64 days following the first (Solheim 1983a).

Fledging

The nestling period extends from 28-36 days (average 31.7) (Korpimaki 1981). First-hatched young stay in the nest an average of 2.3 days longer than the last hatched because adults feed young in the nest less when siblings beg outside the nest. In Idaho, the older nestlings left 27-32 days after hatching (Hayward 1989).

Mating System and Sex Ratio

The boreal owl's mating system has not been studied thoroughly in North America. Therefore, the differences in mating systems described for the New and Old Worlds may be artifacts of research emphasis rather than true biological differences. Boreal owls are considered monogamous for the duration of a breeding season in North America. The pair bond lasts only a single season; most individuals nest with a new mate each year. Extra-pair copulations have not been observed. In Europe, polygyny has been observed in most regions and is recognized as an important aspect of the species' mating system (Solheim 1983a, Schelper 1989, Korpimaki 1991). In Scandinavia and Germany, bigyny (male mated to two females), trigyny (male mated to three females), and biandry (female mated to two males) coincide with vole peaks (Solheim 1983a, Schelper 1989, Korpimaki 1991). An estimated 10-67% of males are polygynous in good years but polygamy was never recorded in poor years (Carlsson *et al.* 1987). In two good vole years, bigynous males reared an average

of 7.8 and 9.5 fledglings compared to 4.2 and 5.1 for monogamous males. Males achieve polygamy through polyterritorial behavior, advertising at multiple (up to 5) cavities within the home range (Carlsson 1991). Primary and secondary females were separated by an average of 1,050 m (median, $n = 17$) (Korpimäki 1991). Bigynous males feed primary and secondary females equally during laying but favor primary females during the brooding period (Carlsson *et al.* 1987). Secondary females produce fewer young than their primary counterparts (2.8 vs. 5.1 and 3.3 vs. 6.2 in two years, Carlsson *et al.* 1987). Biandrous females (multiple broods with the same male not recorded) cease caring for the first brood about three weeks after the young hatch (normal end of brooding) and may begin a second clutch with a new mate prior to departure of the first brood (Schelper 1989). The interval between clutches ranges from 50-64 days, the distance between nest sites ranges 0.5-10 km, and there is no significant difference in the number of eggs or mortality of young for biandrous vs. monogamous females (Solheim 1983a).

The sex ratio of adult boreal owls has not been estimated in North America. In Europe, where long-term studies of population ecology are more common, sex ratio of breeding individuals was estimated as 8:10, 0:10, 5:10, and 4.3:10 (females to males) during 4 years in northern Sweden using autumn playback and mist-net trapping (Carlsson 1991). These estimates may be biased, however, by sexual differences in response to playback of primary song.

Nest Site

Nest

Boreal owls nest exclusively in secondary tree cavities—in North America primarily pileated woodpecker, common flicker, or natural tree cavities or in artificial nest boxes. Boreal owl populations are likely limited in portions of their range by availability of cavities.

Maintenance or Re-Use of Nests

In Colorado, 2 (of 6 observed) nests were used 2 years in succession (R. Ryder, Colo. State Univ., Ft. Collins, CO). Both instances were in natural cavities in lodgepole pine. The owls were not captured so whether the same or different birds used the nests was unknown. Natural nest cavities were never used 2 years in succession in Idaho and rarely used again by the same individual (Hayward and Hayward 1993). Nest cavities may be reused by different individuals but generally after a "rest" period of more

than one year. Nest boxes in Idaho have been occupied in successive years but only by new individuals and after the box was cleaned. In Europe, where cavities are more limited, repeated use of nest boxes is more frequent (Sonerud 1985, Korpimäki 1988a).

Nesting

Egg Laying and Care of Young

Clutches in Idaho were begun 1-19 (usually about 6) days after the female occupied the cavity. In Finland, eggs were laid at intervals of 48 hours but varied from 0.3 to 0.7 eggs per day (Korpimäki 1981). The female does all incubation. There are no reports of egg dumping.

Brooding is performed exclusively by the female beginning immediately after hatching and lasting until the oldest nestling reaches 20-24 days. During the first 3 weeks the male brings all food to the nest for the female and young and the female feeds the young. The male continues to provide for the young throughout the nestling stage and the female supplies food to nestlings after ceasing brooding at some nests. After fledging the young are dependent on the adults for food for over a month.

Growth and Development

Variation in clutch size is reported under Demography, below. During the nestling period, which lasts 30 days for most young, nestlings gain about 5.2 g per day with the greatest absolute gains from 8-13 days (10 g/day). Young reach adult mass by 14-17 days; at 30 days nestlings average 156 (± 21.3 ; $n = 5$; range 130-174 g) (Hayward and Hayward 1993).

DEMOGRAPHY

Life History Characteristics

Age of First Reproduction

Banding records in the northern Rocky Mountains indicate that boreal owls breed the year after hatching. More intensive study in Finland indicates that, except in years of reduced food availability, both sexes can breed the year after hatching, but a larger proportion of females than males breed their first year (Korpimäki 1988c). Over an 8-year period, 16% of first-year males and 65% of second-year males bred (Korpimäki 1992). Both sexes are capable of breeding each year, but prey availability determines individual status year-to-year (Korpimäki 1988c). Second broods are not reported in North America;

see the Mating System and Sex Ratio section under Breeding Biology.

Clutch

Variation in clutch size is one of the most studied aspects of the species' biology, particularly in Europe. These studies have established that the number of eggs laid by boreal owls varies in relation to environmental conditions, particularly prey availability. Clutch size varies among geographic regions, among years, and among individuals within years. In both Europe and North America, northern populations that prey on fluctuating vole populations display the greatest variation in clutch size and have the largest potential clutches (Bondrup-Nielsen 1978, Korpimäki 1986a, Hayward *et al.* 1993) (table 4). Over 17 years, mean clutch size varied from 4.3 to 6.7 in western Finland (Korpimäki and Hakkarainen 1991) and over 4 years in Idaho from 2.5 to 3.5 (Hayward *et al.* 1993). The dramatic variation in clutch size within and among years is further shown in table 4.

Korpimäki (1987b, 1989) and Hornfeldt and Eklund (1990), using experimental and observational studies, demonstrated the direct link between vole abundance and clutch size in Finland. Further support for this pattern comes from observational studies in Norway (Lofgren *et al.* 1986), Sweden (Sonerud 1988), Germany (Schelper 1989), France (Joneniaux and Durand 1987), and Idaho (Hayward *et al.* 1993). Each of these studies reported larger clutches in years when indices of small mammal abundance, based on snap or live-trapping, were high.

To further demonstrate the variation in clutch size that has been observed I provide additional summary statistics from a sample of studies. Clutch size for separate populations in Idaho averaged 3.25 (± 0.42 SD, $n = 11$, range = 2-4) and 3.57 (± 0.34 SD, $n = 31$, range = 2-5) (Hayward *et al.* 1993, Hayward, G. D. and P. H. Hayward, unpubl. data) (table 4). From

a similar latitude in Europe (Germany), Schelper (1989) reported clutches of 3-4 eggs with larger clutches in years when voles dominated the diet. An earlier study in Germany reported 34 nests averaged 3.8 eggs (Konig 1969). In Finland, pooling results from 2 areas over 12 years shows clutches averaging 5.6 (± 0.13 SD, $n = 412$, range = 1-10) (Korpimäki 1987b).

Fledging Success and Population Productivity

Patterns of fledging success reported for boreal owls in Europe and North America reflect the patterns reported for clutch size. Experimental and observational results strongly support the contention that prey availability influences fledging success and overall population productivity (e.g., Korpimäki 1987b, 1989, Hornfeldt and Eklund 1990). Therefore this section will not repeat results that simply duplicate those reported but will note important differences. Representative fledging rates include: 2.3 (± 0.54 SD, $n = 6$, range = 2-3) fledglings/successful nest in Idaho (Hayward 1989); 3.4 young/nest in Germany (Konig 1969); and 3.2 fledglings/nest and 3.9 fledglings/successful nest over a 14-year period in Finland (Korpimäki 1987b).

Korpimäki's (1988d) studies in western Finland suggest that fledging success is more strongly influenced by prey availability during decrease and low phases of the vole cycle. Clutch size, in contrast, is more sensitive to prey availability during the increase phase.

Korpimäki (1988c) has also shown that breeding performance in Tengmalm's owl is dependent on the experience of both members of the breeding pair; pairs of older birds experience the highest productivity. These data suggest that annual reproductive success increases over time, within individuals.

Fledging success is usually reported as the mean

Table 4.—Summary of reproductive statistics for boreal owls from sites in North America and Europe.

Location ¹	Median laying date	Range laying dates	Mean clutch size	Mean no. young fledged ²
Colorado	10 May	17 Apr-1 Jun		
Idaho	1 May	12 Apr-24 May	3.25	2.3
Minnesota		30 Mar-12 Apr		
Alaska	10 Apr	27 Mar-5 May		
Finland	3 Apr	23 Feb-7 Jun	5.6	3.9
Germany			3.8	3.4

¹Sources of information: Colorado (Palmer 1986), Idaho (Hayward 1989), Minnesota (Lane 1988), Alaska (T. Swem, U.S. Fish & Wildl. Serv., Fairbanks, AK), Finland (Korpimäki 1987b), and Germany (Konig 1969).

²Calculated only for successful nests.

number of fledglings per successful nest. Productivity, however, is strongly influenced by nesting success (rate of unsuccessful nests). In some years, the small proportion of the population breeding has a greater impact on productivity than reduced clutch size or fledging success.

In central Idaho, 10 of 16 nests produced no young in a study where all but one nest was a natural cavity (Hayward 1989). In Norway, during a 13-year study employing nest boxes, 48% of 101 clutches were lost to predation (Sonerud 1985). A nest box study in Finland reported 85% of eggs hatched and 53% of the eggs laid ($n = 890$) produced a fledgling, averaging 3.2 fledglings/nest and 3.9 fledglings/successful nest over 14-year period (Korpimäki 1987b).

The influence of owl density on reproduction has not been directly addressed in the literature. The patterns described above do not suggest strong inverse density dependent reproduction. Clutch sizes and fledging rates tend to be highest in years when prey is abundant and the greatest number of owls are breeding. These results, however, do not preclude the potential for density dependent limitation of population growth. Perhaps density dependence is determined by the number of adult owls breeding per 1000 voles per km^2 . Because prey availability is a primary factor influencing reproduction, and boreal owls consume up to 17% of available *Microtus* (Korpimäki and Norrdahl 1989), a feedback loop is available to self-limit population growth to some degree. As discussed below, however, territoriality is not likely to be a mechanism for density dependent self-limitation.

Lifetime Reproductive Success

Lifetime reproductive success is difficult to study in any mobile vertebrate. No studies in North America have examined this topic. Based on 11 years of data, lifetime reproduction (LR) of 141 males in Finland varied from 0-26 fledglings (mean 5.2); 21% of males reared 50% of all fledglings (Korpimäki 1992). Among males hatched in a given year, 5% produced 50% of fledglings in the next generation. Offspring survival from egg to fledgling, lifespan of individual, clutch size of nests, and phase of the vole cycle at which an individual entered the populations were important components of LR for individual males. Offspring survival (as represented by the number of fledglings per nest) varied from 0 to 7. Most males breed for only a single season but the number of seasons ranged from 1-7 years ($\bar{x} = 1.5$). Clutch sizes varied from 2-8. Finally, the temporal variation in habitat quality due to fluctuating vole abundance was the most important environmental

determinant of LR. Males entering the population in the low and increase phases of the cycle had larger LR than those entering in decrease or peak (individuals raised in the low and increase phases had better food conditions in their first 1-2 years of breeding). The extreme variation among individuals in lifetime reproductive success is expected because prey availability varies greatly among years and within years among breeding sites in Finland. Other vertebrates exhibit similar patterns (e.g., Clutton-Brock *et al.* 1982, Grant and Grant 1989).

Proportion of Population Breeding

Sound estimates of the number of non breeding individuals are not available. Indirect evidence from North America and Europe, however, demonstrates extreme yearly variation in breeding attempts; e.g., in Sweden, nest box occupancy in one area varied from 0.8% to 40.2% in 1980-81, and 39.4%, 0.8%, and 23.8% in 1982-84 (Lofgren *et al.* 1986). In Idaho, the number of calling males heard per kilometer surveyed varied from 0.02 to 0.24 from 1984 to 1987 and some radio-marked individuals did not breed even in good breeding years (Hayward 1989).

The most direct estimates come from Korpimäki's studies based on 10 years of monitoring his smaller study area (100 km^2 , Korpimäki and Norrdahl 1989). The number of non breeding males (based on singing males who did not nest) varied from 0 to 66% of the population and averaged 47%.

Survivorship

In Idaho, adult annual survival estimated from 25 radio-marked birds was 46% (95% confidence interval 23-91%) (Hayward *et al.* 1993). In Finland, based on 281 banding recoveries, first-year male annual survival was 50% (95% confidence interval 43-57%) and adult male annual survival was 67% (95% confidence interval 61-75%). Based on retrapping birds for 11 years in an intensive study area, 78% of fledgling males died before their first breeding attempt (Korpimäki 1992). In Germany, results of a long-term banding study in an area with natural and artificial nest sites suggested juvenile survival of 20% and adult survival of 72% (Franz *et al.* 1984). In Norway, Sonerud *et al.* (1988) estimated 62% adult annual survival.

Breeding males remain in the breeding population an average of 1.5 (range = 1-7) years (Korpimäki 1988c) with an average life span of 3.5 (range = 2-11) years (E. Korpimäki, pers. comm.). In Germany, females in a nest box study were documented living 8 ($n = 6$), 9 ($n = 5$), and 10 ($n = 1$) years (Franz *et al.* 1984).

Ecological factors influencing survival have not been explored in any detail. Korpimäki (1992) established that owls in his population survived in the breeding population longer during increase than decrease phases of the vole cycle. Although starvation is often presumed to be a major mortality factor, direct and indirect causes of mortality have not been identified for any populations.

Movements as Related to Demography and Metapopulation Structure

As described earlier, boreal owls usually remain resident within a multiannual home range but are capable of moving long distances between breeding sites. In Sweden, young females that bred the year after fledging moved 24 km (median) from their natal territory while males moved less far (median 4.5 km). In Finland, adult females disperse up to 580 km (median 4 km) between successive breeding seasons while males rarely move more than 5 km (median 1 km; Korpimäki *et al.* 1987). During prey declines, more than half of females in Sweden were nomadic (Lofgren *et al.* 1986). Adult nomadism occurs in response to prey shortage, which may be more acute and regular in northern geographic areas. Juvenile boreal owls frequently remain within the same breeding population but also have been documented moving long distances. Research methods are biased toward detecting residency, however, so movements between populations may be quite common. Both adult and juvenile movements have not been studied carefully in North America so inferences concerning the influence of movements on demography stem from European studies.

The nomadic life history of boreal owls and the capacity for juveniles to disperse long distances may result in a strong metapopulation structure within North America. Suitable habitat in the western United States occurs in numerous patches separated by tens to hundreds of km (figure 1). The habitat distribution, then, provides a landscape that will support small populations each separated by distances greater than the normal daily movement and normal yearly movement distances of individual owls. Linkage among populations, then, results from the nomadic movement of adults or exceptional long distance dispersal of some young owls. Subpopulations of boreal owls that occur in disjunct locales may be linked through nomadic movements and juvenile dispersal. These movements are potentially important in the species' population dynamics. Individual populations may act alternately as sources and sinks depending on the status of prey, cavity

availability, weather events, predators, and competitors. The long-term persistence of individual populations may be determined in large part by the rescue effect (Brown and Kodric-Brown 1977) resulting from interpopulation movements of owls, particularly experienced breeding adults.

Local Densities

There are no reliable estimates of population density for boreal owls in North America. Estimates from Europe all refer to breeding season populations, rarely include estimates of non-breeding individuals (Korpimäki and Norrdahl 1989), and most frequently refer to calling male owls. Korpimäki and Norrdahl (1989) for the period 1977-1987 reported a minimum of 1 breeding pair and 2 non-breeding males, and a maximum of 26 breeding pairs and 8 non-breeding males within a 100 km² study area in western Finland.

Indices of density based on calling surveys or number of active nests exhibit extreme yearly variation that corresponds with fluctuating indices of rodent abundance. Density estimates include: 0.6-1.3 nests/km², averaging 0.25/km² in France (Joneniaux and Durand 1987); 0.05-0.46/km² with some small areas as high as 4/km² in Southern Lower Saxony (Schelper 1989); and 0.19 to 0.48/km² in Sweden (Källander 1964).

Spacing and Population Regulation

Behavioral interactions, particularly territoriality, function to limit population size in many bird species (e.g., Hensley and Cop 1951, Krebs 1971, Watson and Moss 1980). Studies in Europe and North America suggest that under most circumstances, territoriality has no influence on abundance of boreal owls. The direct effects of prey abundance and cavity abundance are the most likely factors influencing population size; however, the links between these and other proximate factors are not established. Figure 5 displays the array of environmental factors thought to affect boreal owls based on the studies discussed in this report.

Spacing

Individuals, including mated pairs, are seldom found together except during courtship rendezvous at the nest site. Five mated pairs radio-marked prior to nesting in Idaho roosted within 150 m of one another on 7 occasions (n = 121) (Hayward *et al.* 1993); 1 pair accounted for 4 of these observations. Locations where paired individuals roosted together oc-

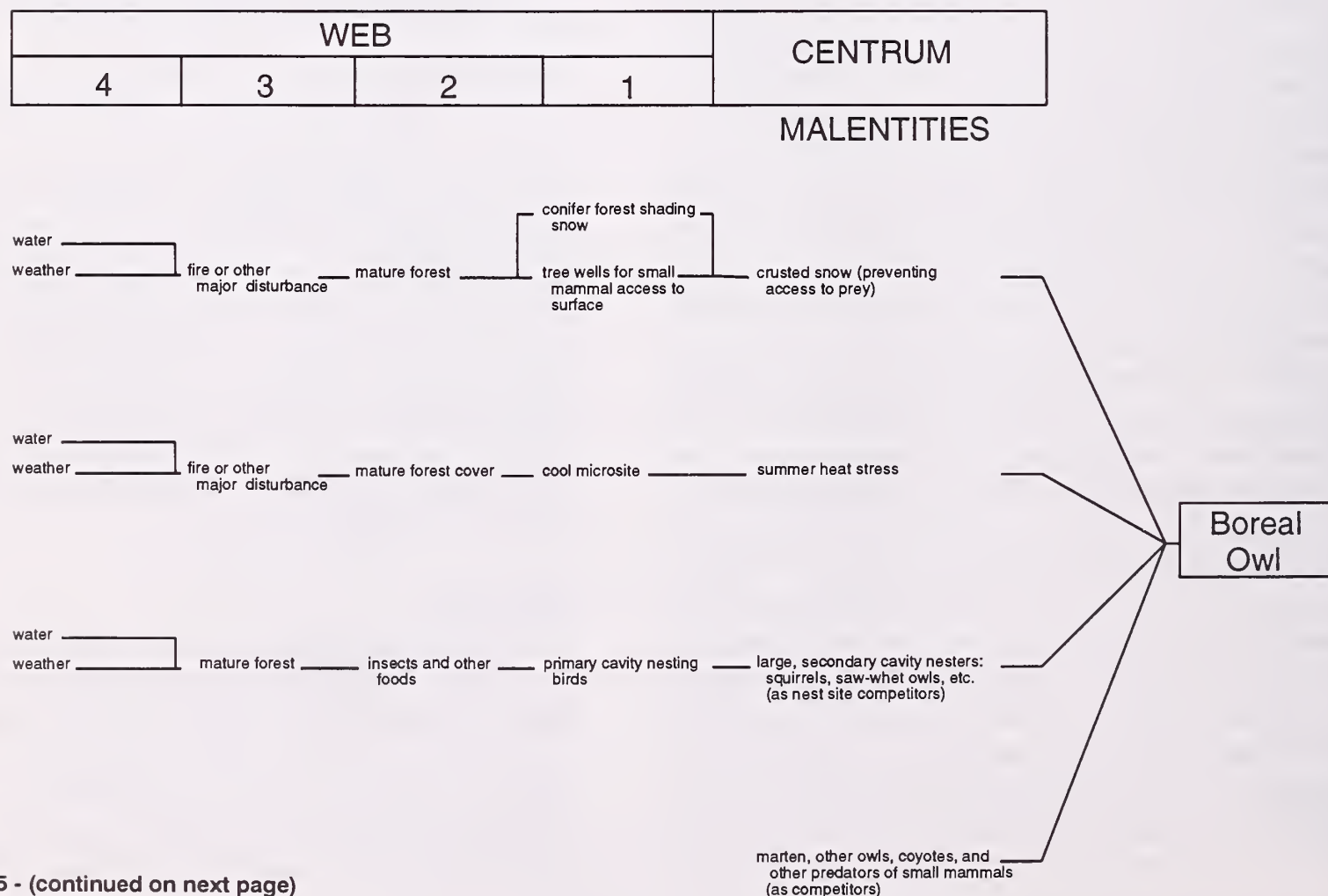
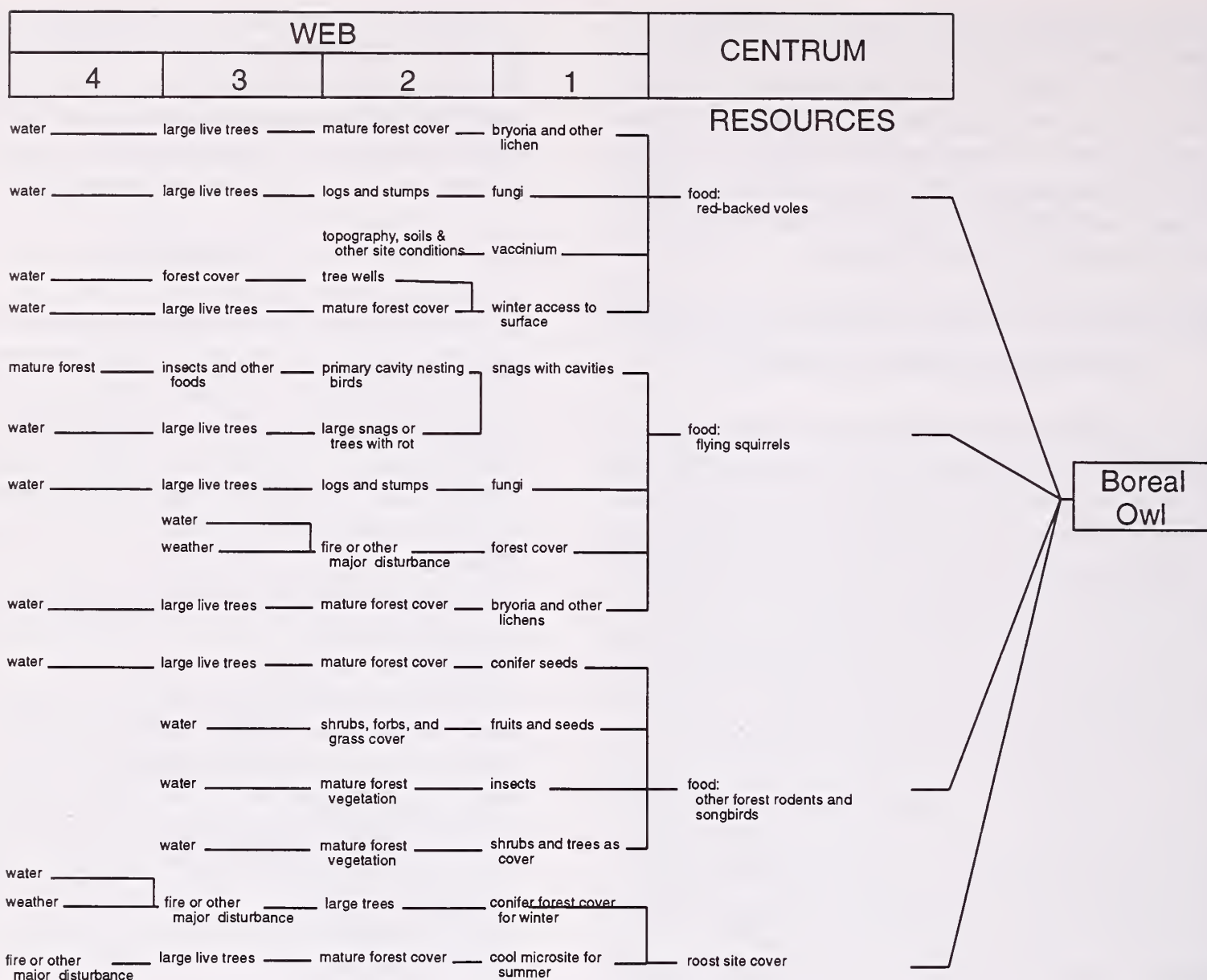


Figure 5 - (continued on next page)

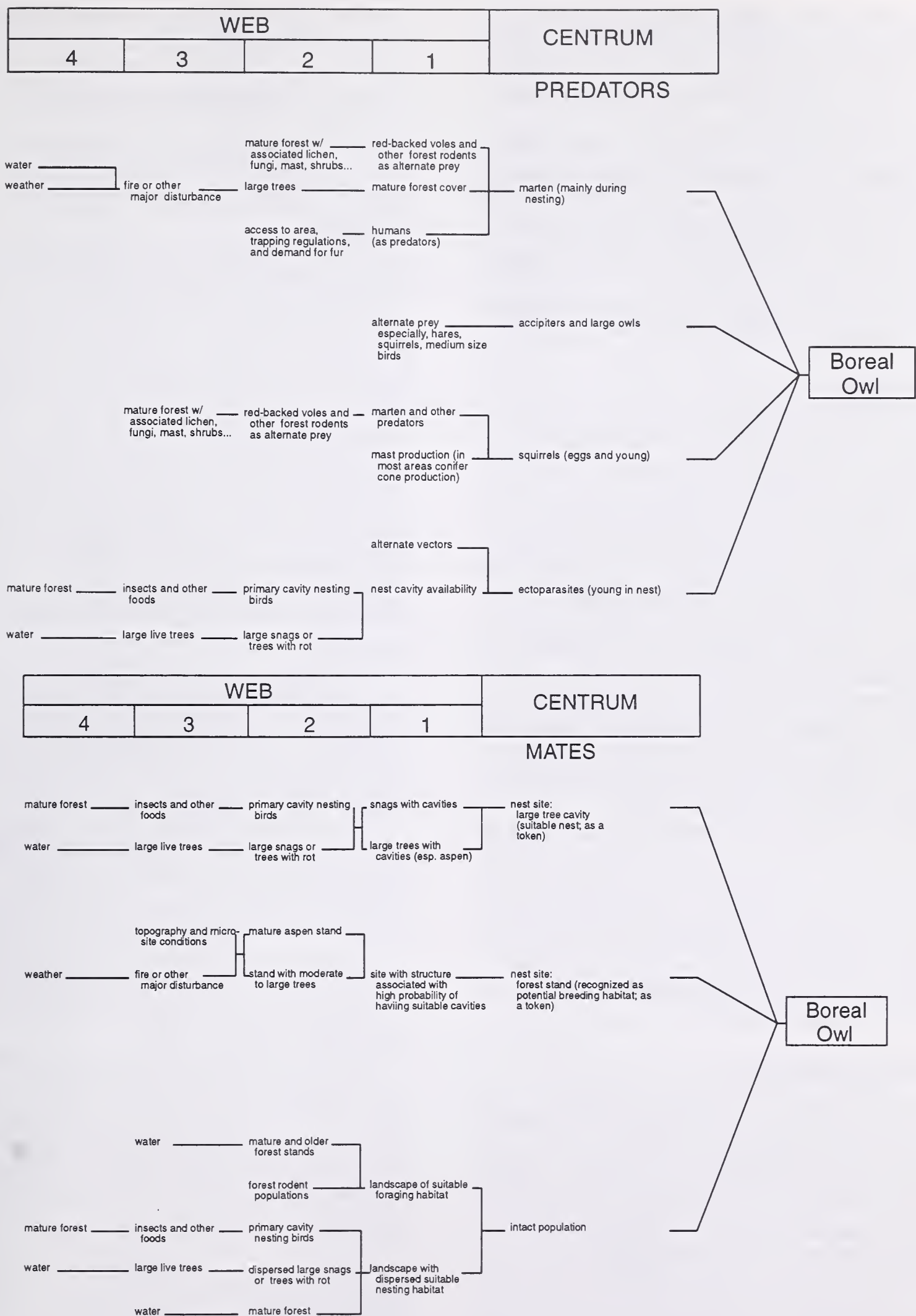


Figure 5.—Envirogram representing the web of linkages between boreal owls in the western United States and the forest ecosystem they occur in. This web should be viewed as a series of hypotheses based on the ecology of boreal owl as described throughout this assessment. For more on the application of envirograms in conservation biology see Andrewartha and Birch (1984) and Van Horne and Wiens (1991).

curred up to 6.5 km from the nest and never at the nest (Hayward *et al.* 1993). Unmated owls were located within 150 m of one another on 2 occasions: 2 males in May and an unmated male and a female caring for young in June.

Although individual owls rarely interact closely, home ranges of individuals living in the same drainage overlap extensively. In Colorado, Palmer (1986) observed > 90% overlap in ranges of two males. In Idaho, ranges of 13 owls monitored in two adjacent drainages overlapped another owl's by at least 50% and the degree of overlap was not dependent upon sex (Hayward *et al.* 1987b and Hayward *et al.* 1993).

Territoriality

Boreal owls do not exhibit strong territorial behavior. Males sing to maintain a territory only in the immediate vicinity of potential nest cavities. Territory defense is confined to the nest site and seems to include less than a 100-m radius around the nest (Mikkola 1983). Carlsson (1991) reports a male calling within 200 m of another male's nest. The paired male flew within 50 m of the calling bird and uttered a "screech" call but did not pursue the caller. Minimum distances reported between nests were 100 m (Mikkola 1983) and 0.5 km (Solheim 1983b). The distance between territories depended on prey abundance (Schelper 1989, Korpimäki and Norrdahl 1989). How factors other than prey abundance (e.g., cavity availability, habitat structure) influence territorial spacing has not been studied.

Territorial behavior is thought to be confined to the courtship and breeding period (January - July), but Kampfer-Lauenstein (1991) reported warning calls and direct flight attacks (suggesting territorial behavior) in response to playback from August-November. This suggests that the autumn territory is within the year-round home range but may not coincide with breeding territory.

Population Regulation

The availability of nest cavities and prey are the most likely environmental factors to limit populations of boreal owls (when populations are limited). The role of prey availability in observed nomadic movement patterns and the yearly variation in productivity suggests that food may regulate boreal owl abundance at times in some locales. The mechanism of limitation by food is not completely understood; but prey available to the female prior to nesting may be a critical factor in laying date and clutch size. Prey availability during the nestling period strongly influences the number of young fledged (Korpimäki 1989, Hornfeldt and Eklund 1990). Large clutches

have been shown to produce more young leaving the nest (Korpimäki 1989). In his 1989 paper, Korpimäki reported an experiment in which he manipulated the abundance of food available to females prior to laying during a peak in the vole cycle. Despite the abundance of natural prey, females provided additional prey laid earlier, laid larger clutches, and fledged more young than control individuals.

Other investigators, using nonexperimental approaches, have concluded that prey availability has a direct positive correlation with boreal owl productivity (e.g. Lofgren *et al.* 1986, Sonerud *et al.* 1988, Hayward *et al.* 1993). The number of owls nesting (Lofgren *et al.* 1986), laying date (Hörnfeldt and Eklund 1990), clutch size (Lofgren *et al.* 1986), nest abandonment (Hayward *et al.* 1993), number of fledglings (Hayward *et al.* 1993), and movements of individuals following nesting (Sonerud *et al.* 1988) have all been linked with abundance of small mammals. Prey limitation leads to nomadic movements and likely results in higher mortality.

These demographic data have not been incorporated into a model (verbal or quantitative) describing population growth. Whether the absolute abundance or changes in prey populations is more important has not been pursued. Neither have the links between prey availability and changes in other environmental features been explored. And finally, the role of stochastic events in the pattern of population change has not been addressed.

In some areas of Europe, natural cavity availability is thought to limit population size and distribution (Korpimäki 1981, Franz *et al.* 1984). In North America, in regions with few (or no) pileated woodpecker or flicker cavities, nest site availability may limit boreal owl abundance. Within the geographic range of pileated woodpeckers, the absence of the woodpeckers at higher elevations may limit abundance (Hayward *et al.* 1993).

Cavity availability and abundance of prey likely interact to influence boreal owl population growth. Tree cavities occur nonrandomly across the landscape as do small mammal populations. The spatial arrangement of cavities and prey (in relation to one another) are important in determining boreal owl abundance.

Other factors potentially play a role in boreal owl population growth but research has not addressed these possibilities. Indirect evidence suggests that the owl's southern distribution and its lower elevation range in montane areas may be related to summer heat stress (Hayward *et al.* 1993). Boreal owls are easily heat stressed and seek cool roost locations

in summer. The owl's physiological response to heat stress has not been measured, however.

COMMUNITY ECOLOGY

Predation on Boreal Owls

Marten (*Martes* spp.) are the most important predator of owlets and adult females at the nest site. Over 13 years, 48% of clutches were preyed upon in Norway, most by marten (Sonerud 1985). In Idaho, loss of nests are also most frequently attributed to marten; red squirrel (*Tamiasciurus hudsonicus*) predation upon eggs is also suspected (Hayward, G. D. and P. H. Hayward, unpubl. data). Aside from predation by marten at the nest, Cooper's hawk (*Accipiter cooperi*), northern goshawk (*Accipiter gentilis*), great-horned owl (*Bubo virginianus* or *Bubo bubo*), Ural owl (*Strix uralensis*), and tawny owl (*Strix aluco*) are the most important predators of young and adults (Herrera and Hiraldo 1976, Mikkola 1983, Reynolds *et al.* 1990). Research has not examined the impact of predation away from nests on population dynamics.

Relationship With Prey Populations

As described earlier, small mammal abundance has a direct and significant impact on boreal owl movements, reproduction, and survival. This relationship between prey abundance and boreal owl demography has been studied by several scientists in Europe (e.g., Korpimäki 1984, 1987a, Lofgren *et al.* 1986, Sonerud 1986) and to a lesser extent in North America (Hayward *et al.* 1993). In contrast, the influence of boreal owls on the dynamics of their prey populations has not been studied.

Korpimäki and Norrdahl (1989) provide the only focused discussion of this topic based on a 10 year study in western Finland. This work combined monitoring of owl breeding activity, owl breeding success, owl diet, and small mammal abundance in a 100 km² area. The results suggested that Tengmalm's owls had a direct effect on *Microtus* and to a lesser extent *Clethrionomys* populations. Predation by boreal owls likely dampens fluctuations in vole populations through the combined influence of the numerical and functional response of the owls to changing vole abundance.

Korpimäki and Norrdahl (1989) reported up to a 21-fold year-to-year variation in the number of Tengmalm's owls. Breeding population size was correlated with vole abundance ($r = 0.80$, $P < 0.01$). The nomadic nature of the owls in Finland, their potential to produce large clutches, and a breeding

system that promotes bygamy and biandry in good prey years accounted for the dramatic numeric response that showed no time lag with the vole fluctuations. The owls exhibited a type 1 linear functional response with respect to vole (*Microtus* and *Clethrionomys*) abundance with no leveling off in capture rate even at the highest vole densities. The proportion of *Microtus* in the diet varied from 0-89%.

Combining the observed numeric and functional response of the owl population revealed that the proportion of available *Microtus* and *Clethrionomys* captured was higher in years when voles were most abundant (11 and 8% of the respective mammal populations) than in other years (4 and 5% of the respective mammal populations). Korpimäki's argument that Tengmalm's owl directly impacts the dynamics of its primary prey stems from his data on the owls' demographics and behavior. As a nomadic vole specialist, which can rapidly switch prey, the owl responds rapidly to changes in vole abundance. The owl's functional response indicates a lack of satiation at high vole densities which, when combined with the numeric response, leads to increased predation with increased prey abundance.

South of Finland, Tengmalm's owl is characterized as a resident-generalist, rather than a nomadic-specialist. Korpimäki and Norrdahl (1989) argue that these two life histories lead to similar impacts on fluctuating prey. Therefore, although the results can not be directly generalized to other regions, the evidence suggests that boreal owls may influence prey populations elsewhere.

Competitors

The influence of competitors on boreal owl populations has not been studied. Hayward and Garton (1988) described the pattern of resource partitioning among montane forest owls in central Idaho, and Korpimäki (1987c) described community dynamics in Finland.

Korpimäki (1987c) indicated that boreals were the most numerous species in a spruce forest in locations where populations of Ural owl were scarce. He suggested that Ural owls may limit the density and distribution of boreal owls. In North America, in sympatric situations, there is a potential for exploitative competition (when prey is limited) with saw-whet owls (Hayward and Garton 1988), great gray owls, and maybe most important, American marten (*Martes americana*). The degree to which this competition limits the distribution or abundance of boreal owls is unknown.

Potential competition for nest cavities may have the most direct influence on boreal owl distribution

and abundance. Northern flying squirrel, roosting pileated woodpeckers, northern hawk owl, and saw-whet owl are the most likely competitors. Again these relationships have not been examined.

BOREAL OWL RESPONSE TO FOREST CHANGE

Individual and population response of boreal owls to forest change has not been studied directly using either experimental or observational studies. Below I interpret the results of studies examining habitat use and population dynamics as they relate to this question. Because much of the knowledge necessary to infer the owl's response has been described in earlier sections, this section is brief in relation to its importance.

Nesting Habitat

As an obligate cavity nester, boreal owl populations may be influenced by changes in cavity availability resulting from changes in snag abundance or woodpecker populations. The strength of the relationship is dependent on the relative abundance of nest sites. Changes in forest structure that reduce the number and dispersion of trees larger than ~45 cm dbh could limit the owls. Similarly, changes in forest structure that alter woodpecker prey availability or the foraging ability of flickers and pileated woodpeckers will affect boreal owl nest site availability. Finally, changes in tree species composition, regardless of tree size class, could influence nest site availability as tree species differ in their longevity as a snag and in suitability for cavities (McClelland 1977).

Because nest cavities are a species requirement, the function relating cavity availability to boreal owl breeding population density is likely a complex curve. In landscapes where nest sites are not limiting, a steady linear reduction in cavities may initially have no impact on the owls. As cavities become less abundant, breeding owls may decline initially, not due to an absolute lack of nest sites but due to the imperfect ability of the owls to locate suitable cavities or due to the juxtaposition of cavities and foraging habitat and their dispersion. As cavities become still more scarce, breeding owl abundance will decline in direct, linear response to the decline in cavity abundance.

Franz *et al.* (1984) demonstrated that cavities were limiting for boreal owls on their study site in Germany. Nest box studies in Sweden, Norway, and Finland also suggest that natural cavities were limit-

ing. Biologists suggest that the long history of forest management that has removed old forest and large trees from Fennoscandia has led to significant natural nest site limitation. Up to 90% of the owls in these studies rely on nest boxes for nesting structures.

Changes in forest structure may also impact aspects of nest quality rather than nest site availability. Nests may become more vulnerable to predation or owls may have more difficulty locating suitable cavities under various forest structures. Results of a small nest box experiment in Idaho (Hayward *et al.* 1993) suggested that the owls prefer old forest sites for nesting. The results were not conclusive, however, and other studies of nesting habitat have been strictly observational (Bondrup-Nielsen 1978, Palmer 1986). The pattern of nest site use does indicate that older forest sites are used for nesting by these owls and therefore nesting opportunities may decline if the distribution of forests change toward younger age classes.

Roosting Habitat

The elimination of forest from a portion of an individual owl's home range will reduce roosting opportunities. The impacts of less dramatic changes in forest structure are not so clear. Observational studies of roosting habitat in Canada and Idaho led to different conclusions regarding the potential impact of forest change. A small sample of roosts and paired random forest sites in Canada did not differ from one another, implying the owls were not selective among the range of available sites (Bondrup-Nielsen 1978). In Idaho, owls did select forest with particular structural features, especially during summer (Hayward *et al.* 1993). Results from this study suggest that a reduction in the abundance or distribution of mature and old spruce-fir forest sites could limit roost sites during summer. Because cool roost locations dispersed throughout the home range may be important in boreal owl thermoregulation, a reduction in the quality of roost sites may influence owl survival rates.

Forest change involving type conversion (shift in tree species composition) could similarly influence roosting habitat. Old spruce-fir forest would provide a greater degree of microhabitat amelioration than old lodgepole pine forest.

Foraging Habitat

Changes in forest structure and/or species composition will influence boreal owls by changing prey abundance or availability. Prey availability will be

influenced by changing the dispersion of hunting perches or the owls' access to prey. Because boreal owls hunt from perches, forest removal affecting patches larger than several hectares will always eliminate foraging habitat even if prey populations are increased. Dense ground vegetation or crusted snow will reduce access to prey.

Sonerud (1986) described the importance of old spruce forest as foraging habitat for boreal owls in Norway despite the lower abundance of small mammals in this habitat. In winter, uncrusted snow facilitated the movement of prey to the snow surface providing the owls access to prey. In summer, the lack of dense forest-floor vegetation provided the owls clear access to small mammals. These results stress the importance of conifer canopy cover in maintaining small mammal availability.

Red-backed voles represent important prey for boreal owls in much of North America (Bondrup-Nielsen 1978, Palmer 1986, Hayward *et al.* 1993). Changes in forest structure or composition that influence red-back vole populations will likely influence boreal owl populations. The effect of forest structure and composition on red-backed vole population dynamics is not well known aside from the decline in red-backed vole populations usually observed following forest removal. Similar knowledge for other prey species (northern flying squirrels, northern pocket gophers, heather voles, etc.) is also lacking.

Broad-Scale Habitat Change

As the reader can well imagine, the influence of regional changes in habitat conditions on boreal owl populations is unknown. Changes at this scale will influence metapopulation structure through dispersal and local extinction. Changes in the size of subpopulations, distance between neighboring subpopulations, changes in productivity of source populations, and characteristics of habitat separating subpopulations likely influence metapopulation stability and would be important to manage on a regional scale.

BOREAL OWL RESPONSE TO HUMAN OR MECHANICAL DISTURBANCE

Boreal owls tolerate human and machine noise. In Colorado, owls have nested within 30 m of a major highway (R. A. Ryder; pers. comm.). In Europe, nests have been located within farmsteads and are associated with agriculture (Korpimäki 1981). Owls tolerate frequent (every 4-5 days) direct nest inspec-

tion (except during laying) and will deliver prey to the nest while humans observe from several meters away. There is no evidence that disturbance is an important factor in nest loss or owl movements.

ASSESSMENT OF SCIENTIFIC BASIS FOR PARTICULAR MANAGEMENT TOOLS

Monitoring

Intensive management of wildlife populations, particularly threatened, endangered, and sensitive species, requires information on population trend of the target species and on habitat trend. Monitoring regional trends in boreal owl populations may be approached intensively or extensively. An intensive approach involves tracking a measure of abundance for sample populations within the target region over time. An extensive approach tracks presence/absence for a large sample of populations over time.

These approaches differ in method and objective. The intensive approach facilitates examination of environmental features associated with trends in individual populations but requires a large field effort, as described below. The extensive approach costs less and tracks the "winking" on and off of populations throughout the region, but it provides no insights into the causes of population changes.

Methods for monitoring boreal owl populations have received little attention. Playback surveys have been used extensively to determine the geographic distribution of the species (Palmer and Ryder 1984, Hayward *et al.* 1987a) and have been promoted as a promising monitoring technique for other owls (Johnson *et al.* 1981, Forsman 1983, Smith *et al.* 1987). Playback surveys cannot be considered the best technique to assess trends in boreal owl populations, however, because many factors influence calling rate. Lundberg (1978) suggested that the number of boreal owls singing may be inversely related to breeding success. He found that "territorial and breeding pairs were more silent than non-territorial individuals" and concluded that "censuses made at roadside stops give unacceptable results for population studies of both the Ural owl and Tengmalm's [*boreal*] owl" (Lundberg 1978:171).

Although Lundberg's (1978) results suggest that playback surveys should not be used for intensive population monitoring, playback could be useful in developing methods of presence/absence monitoring. Playback methods seem to be the most efficient method to determine the occurrence of boreal owls in an area. These provide the basic data necessary in

a presence/absence sampling design. Research to date has not explored the potential of these techniques for monitoring owls on a regional basis. These methods would fit well into a scheme designed to approach management in a metapopulation framework.

Some work has been done to develop more intensive population level monitoring. Hayward *et al.* (1992) examined the sampling efficiency of employing nest boxes to monitor response of boreal owls to changes in foraging habitat. The results suggest that when boreal owls are moderately abundant (nest box occupancy >7%), modest changes in clutch size and occupancy rate could be detected with a system of 350 nest boxes. When owls are less abundant, the number of nest boxes necessary to detect modest changes would be prohibitively large. Research has not addressed the underlying assumptions of the methods suggested in this study (Hayward *et al.* 1992).

An understanding of boreal owl vocalizations is necessary in designing surveys to determine distribution or to develop a presence/absence monitoring program. Difficulties observing behaviors associated with vocalizing boreals and problems interpreting phonic representations of calls have led to some confusion in describing the array of sounds produced and the function of various vocalizations. Authors within the United States and in Europe have used a variety of names to describe vocalizations and no one set of names is preferable. Meehan (1980) and Bondrup-Nielsen (1984) provide the most complete vocal analysis for the boreal owl. Cramp (1977) and Johnsgard (1988:221) summarize information for North America and Eurasia. Throughout this discussion I refer to Meehan (1980) as RHM and Bondrup-Nielsen (1984) as SBN.

The call most important in terms of management is the primary song (staccato song--SBN, song--RHM). This is the call that can be attributed most certainly to boreal owls and is the call most frequently elicited in springtime playback surveys. The primary song is uttered loudly only by males from a perch near a potential nest cavity, is not commonly used outside the breeding season, and isn't used during antagonistic encounters among individuals. It is presumed to function in mate attraction as a long distance advertisement song. The call is a loud vocalization uttered as a series of trills consisting of 11-23 notes at ~0.74 kHz that increase in volume during a trill lasting 1.8 (1.32-2.32) seconds (SBN). The trill is repeated after a silence of 1 to several seconds; singing bouts frequently last 20 minutes but may extend 2-3 hours with infrequent pauses of sev-

eral minutes. The song is frequently heard by humans over 1.5 km and up to 3.5 km.

Singing in Idaho began by 20 January, reached greatest intensity by late March, and became uncommon by late April (Hayward 1989). In Colorado, Palmer (1987) reported singing 18 February - 21 June; singing peaked in late April and a lull followed in early May with renewed frequency late May through June. Palmer (1987) speculated that calling in June resulted from first-time breeders and unmated males. In Alaska, singing peaked by mid-February to March (RHM).

See Hayward and Hayward (1993) for a summary of the characteristics of other songs.

Viability Analysis

Biologists working with land management agencies are often asked to evaluate the impact of management activities on sensitive plants and animals. Biologists must document their judgments about whether or not a proposed management action will increase the likelihood of sensitive species becoming threatened or endangered. The basis for the "determination of effect" necessarily involves some kind of population viability analysis (PVA). Gilpin and Soule (1986) described PVA as a complex process of considering all factors that affect the processes of species extinction or persistence while Boyce (1992) discussed both theoretical and practical aspects of PVA.

Tools necessary to conduct PVA for boreal owls are not available. Neither mathematical nor word models linking the relevant factors have been developed. Furthermore, the ecological understanding of the owl's ecology in North America has not reached the level of maturity necessary to conduct formal viability analyses. The biological and ecological information summarized in this chapter, however, could provide the background necessary to structure assessments for individual impact analyses until more general guidelines for PVA are developed. Further ecological research will be necessary, though, before developing any formal analysis tools.

Effects Criteria Identification

Although PVA is an important tool for impact analysis, the identification of criteria upon which to base statements of effects is important in most environmental assessments. Therefore, guidelines from which to build effects criteria are important for resource managers. These types of guidelines are not currently available to managers. The paucity of in-

formation on boreal owl ecology and life history specific to different management regions precludes development of elaborate criteria. Based on the ecological relationships depicted in figure 5, however, some basic guidelines can be outlined. These will be stated generally here but could be elaborated for particular regions:

(1) Large trees are required for nesting boreal owls.

(2) Primary cavity nesters (e.g., pileated woodpeckers, common flickers) provide a majority of nesting sites in most areas and the status of populations of these birds is important to the productivity of boreal owls.

(3) The availability of small mammals limits populations of boreal owls in many areas; therefore, factors that influence small mammal abundance and availability will directly influence the abundance of boreal owls.

a) Red-backed voles are important prey for boreal owls everywhere the owl has been studied. In the western United States the abundance of red-backed voles is related, at least in part, to forest age, fungi abundance, and lichen abundance.

b) Prey availability is related to forest structure characteristics as the structure influences mobility of boreal owls. Dense shrub cover or high tree density will limit the access of boreal owls to small mammals. Conditions that promote snow crusting (large openings) will also reduce small mammal availability.

(4) In the western United States, boreal owl distribution may be limited, in part, by warm summer temperatures. Cool microsites for daytime roosts may be important in determining the species' current distribution. In Idaho, old forest sites provided cool microsites used for roosting (Hayward *et al.* 1992).

Stand and Watershed Scale Silviculture Prescriptions

Guidelines with which to develop specific stand and watershed scale silviculture prescriptions are not published. Knowledge of boreal owl ecology and habitat choice limits the specificity of any guidelines. As shown above, some general statements can be made with certainty.

Current understanding of boreal owl habitat use suggests that the maintenance of forested landscapes is required for boreal owls. Furthermore, silvicultural prescriptions must provide for large diameter trees well dispersed over space and time. The roosting, nesting, and foraging ecology of boreal owls in the western United States also suggests that mature

and older forest must be well represented in the landscape to support a productive boreal owl population. In most cases, uneven-aged management or other silvicultural practices that maintain canopy structure and forest floor moisture will maintain boreal owl nesting, roosting, and foraging habitat. Forest clearcuts provide little or no habitat for boreal owls for two to several decades after disturbance and may not provide high quality habitat for one to two centuries.

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Dynamics of Subalpine Forests

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INTRODUCTION

The boreal owl's fairly specific habitat requirements restrict its range in the conterminous U.S. to subalpine forests (see Chapter 9). These forests provide tree cavities, uncrusted snow that facilitates preying on small mammals, and cool microclimates essential for summer roosting. Such forests also provide habitat for the owl's prey, which consists primarily of red-backed voles, mice, and other small mammals. Significantly, these prey animals often eat lichens and the sporocarps of fungi. Both are common at high elevations or along drainages in the middle and northern Rocky Mountains, the Blue Mountains, and the northern Cascade Range. This chapter focuses on the distribution, structure, and dynamics of subalpine forests in these areas, with emphasis on the Rocky Mountains.

DISTRIBUTION AND STAND CHARACTERISTICS

North America's subalpine forest ecosystems vary in altitude according to latitude and other geographic considerations. Elevation ranges from about 2,600 m to 3,200 m in the middle Rockies; but is lower (1,300-1,900 m) in the northern Rockies, Blue Mountains, and northern Cascades (Romme and Knight 1981, MacMahon and Anderson 1982, Peet 1988). In all areas, the forests extend downward along drainages. The subalpine fir (*Abies lasiocarpa*) and Engelmann spruce (*Picea engelmannii*) that commonly dominate Rocky Mountain subalpine forests are genetically and ecologically similar to balsam fir (*Abies balsamea*) and white spruce (*Picea glauca*), their boreal counterparts (Elliott-Fisk 1988, Peet 1988). Commonly associated species in the Rocky Mountains include lodgepole pine (*Pinus contorta*) and quaking aspen (*Populus tremuloides*). In the northern Rockies, whitebark pine (*P. albicaulis*) grows near the upper limits of the spruce-fir forests and Douglas-fir (*Pseudotsuga menziesii*) is common at the lower limits.

Mountain hemlock (*Tsuga mertensiana*) and silver fir (*Abies amabilis*) dominate subalpine forest in the northern Cascades and in the northern Rockies west of the continental divide (Daubenmire and Daubenmire 1968, Arno 1979, Franklin 1988). Subalpine fir occurs with these more common trees, but Engelmann spruce is less frequent in the Cascades than in the Blue Mountains and Rocky Mountains. Alpine larch (*Larix lyallii*) and whitebark pine occur at alpine treeline. At lower elevations, probably beyond the normal range of the owl, the forests are dominated by Douglas-fir, western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), grand fir (*Abies grandis*), western larch (*Larix occidentalis*), western white pine (*P. monticola*), lodgepole pine, and other species (Franklin and Dyrness 1973, Franklin 1988). The Blue Mountains do not have western hemlock or western red cedar, but grand fir commonly occurs with subalpine fir, Engelmann spruce, lodgepole pine, and Douglas-fir — at least at lower elevations.

The late-persisting snow cover, cool growing season, and dense canopy of subalpine forests collectively prevent any uniform understory development. Often the shrubs, forbs, grasses and sedges are quite sparse, a feature that probably facilitates predation by the owl during the summer and fall. The understory species are characteristic of moist forests and include *Vaccinium scoparium*, *V. globulare*, *V. membranaceum*, *Pachistima myrsinites*, *Pedicularis racemosa*, *Arnica cordifolia*, *A. latifolia*, *Juniperus communis*, *Calamagrostis rubescens*, *Pyrola secunda*, *Carex geyerii*, *C. rossii*, and numerous others (10-45 spp/0.1 ha; Peet 1988). At lower elevations the understory species are different and become quite tall and dense. For example, *Menziesia ferruginea*, *Rhododendron albiflorum*, and *Ledum glandulosum* form an understory that can be 2 m tall in the Cascades and parts of the northern Rockies (Franklin and Dyrness 1973, Franklin 1988). Such forests probably provide lower quality foraging habitat for the boreal owls because of more dense cover for their prey.

Complementing the vascular plants, lichens also

can be quite common, especially in the Pacific Northwest and the mountains of Idaho and Montana. *Bryoria* spp. comprise most of the arboreal lichen biomass, which can be substantial. Lichen biomass ranges from 19 to 35 mt/ha in stands dominated by either subalpine fir or silver fir (Rhoades 1981). The lichens grow as epiphytes on trees; but they are available to small, terrestrial mammals when twigs, branches, or entire trees fall to the ground. The growth of lichen taxa that are important for small mammals apparently depends on forest microclimate (Hale 1983, Lesica *et al.* 1991, Hayward and Rosentreter 1994). Besides shade, subalpine forests provide abundant surface area for lichen establishment; and as the lichens grow, still more surface area is created for the interception of rain. Also, the lichens add surface area on which water condenses when clouds move through the canopy, as often happens at high elevations. Drier forests typically have less lichen biomass, which means fewer small lichen-eating mammals, and therefore potentially less abundant prey for boreal owls.

Stand-replacing fires only infrequently burn subalpine forests, and most of the dominants tolerate the shaded understory environment. These two factors eventually lead to an all-aged or uneven-aged, multi-layered forest. Trees grow to large sizes for the species and site conditions, often persisting as snags for many years after their senescence (Mielke 1950). Such features, along with frequent canopy gaps and abundant wood on the forest floor, are characteristic of old subalpine forests (Kaufmann *et al.* 1992). Many animals in such forests depend, directly or indirectly, on energy flow through food webs based on forest floor detritus.

Comparing Subalpine and Boreal Forests

The boreal forests of Canada and Eurasia often have a species composition and uneven-aged forest structure that is similar to subalpine forests. Balsam fir and either white spruce or black spruce (*Picea mariana*) are the dominant species (Elliott-Fisk 1988). Also, even-aged, seral forests dominated by jack pine (*Pinus banksiana*) are widespread. Jack pine can have serotinous cones and apparently fills the same ecological niche as lodgepole pine in the Rocky Mountains. Aspen and paper birch (*Betula papyrifera*) are found locally in moist upland habitats, and black spruce and tamarack (*Larix laricina*) are abundant in bogs or muskegs (along with sphagnum moss and a variety of ericaceous shrubs). While similar in many ways, subalpine and boreal forests differ in terms of climate and continuity.

The climate is more humid in boreal forests than in some subalpine forests, especially those on the leeward side of major divides. Lower atmospheric pressure at higher elevations causes more rapid evaporation and drying than near sea level where the boreal forests usually occur (Smith and Geller 1979), though frequent rainfall in the subalpine zone could negate this influence of atmospheric pressure. However, the generally more humid nature of boreal forests is suggested by forest classifications based on mosses as well as on trees and other species (Elliott-Fisk 1988). This classification scheme is not commonly practiced in subalpine forests. The more humid nature of boreal forests also leads to abundant lichens that contribute significantly to the food web of the boreal owl.

Subalpine and boreal forests also differ by their degree of continuity or in patch size. Elliott-Fisk (1988) noted that closed boreal forests have a uniform structure over large areas. That might be expected in areas with relatively little variation in topography and elevation and larger average fire size. In contrast, subalpine forests commonly exist as small patches in ravines or only on certain mountain slopes.

The physical characteristics of the dominant trees in both subalpine and boreal forests vary greatly among regions and across different site conditions. Shallow soils at higher elevations (subalpine forests), or higher latitudes (boreal forests), will not produce trees that are as tall as on warmer or more mesic, nutrient-rich sites. Total tree basal area may be high in some stands, approaching 70 m²/ha (Peet 1988), but this too varies greatly with environmental conditions and time since last disturbance. Old forests used by boreal owls probably have tree densities that range from 1,000-2,000 trees/ha and basal areas that range from 50-70 m²/ha. The diameter of dominant trees will be greater where stand-replacing disturbances are less frequent, with spruce in subalpine forests sometimes reaching diameters of 1.5 m and ages over 600 years (Oosting and Reed 1952). Usually, fir does not live much more than 250-300 years and does not grow to be much larger than 50-75 cm dbh. Tree heights might be greatest (sometimes up to 30 m or more) in subalpine forests growing in ravines at lower elevations, where wind and other environmental conditions are moderate and the fire-return interval is long (Romme and Knight 1981).

Boreal forests typically have smaller trees than subalpine forests because of more frequent fires. The greater fire frequency results from fewer topographic barriers, which increases the probability of burning over a much larger area. Most fires are quite destruc-

tive to both subalpine and boreal forests because of the abundant fuel that accumulates by the time spruce, fir and other climax species are dominant.

SUBALPINE FORESTS SINCE THE PLEISTOCENE

During the Pleistocene Epoch, glaciers covered much of the subalpine region where boreal owls now thrive in the Rocky Mountains and northern Cascades. Next to the glaciers, tundra vegetation dominated large areas (Baker 1983, Franklin 1988, Whitlock 1993). Subalpine forests, and presumably the boreal owl, might have extended their range to lower elevations or much further south than they do today; or possibly, they were restricted to small isolated groves that were not covered by ice. Whitlock (1993) concluded that most of the shifts in species composition were altitudinal rather than latitudinal. She also concluded that, about 11,500 years before present (ybp), the climate was 5-6° C colder and alpine treeline was about 600 m lower than it is today (Whitlock 1993). As the ice retreated, an open spruce parkland developed and persisted for about 1,000 years. Subalpine forests began to develop over large areas about 10,500 ybp (perhaps 12,500 ybp in the Cascades). The warmer, drier altithermal (hypsithermal) caused reduced densities of spruce and fir for a 4,000-5,000 year period (9500-5000 ybp); but these trees expanded again following the initiation of the Little Ice Age about 4,000 years ago (Whitlock 1993). Still, subalpine forests cover smaller areas than the forests at lower elevations and they often occur in isolated groves. Moreover, it seems clear that subalpine forests have changed substantially during the last 10,000 years. Owl populations surely changed as well.

Looking to the future, global warming (regardless of the cause) undoubtedly would push subalpine forests to higher elevations or latitudes, thereby restricting the land area that they now cover (Romme and Turner 1990). Of the many owl species, the boreal owl would be affected most adversely by this development in the U.S. because of its association with already patchy high-elevation forests.

SPATIAL DISTRIBUTION OF SUBALPINE FORESTS

A distinctive feature of subalpine forests relevant to boreal owl management is their discontinuous or patchy distribution. Abrupt topographic changes, isolation on the slopes of widely separated mountain peaks or drainages, and periodic stand-replac-

ing disturbances that create seral forests collectively cause this discontinuity (Fischer and Clayton 1983, Bradley *et al.* 1992a,b). Peet (1988) described the nature of disturbance and succession in writing, "... the vegetation is perhaps best thought of not as a uniform stable cover but rather as a mosaic, with the character of each *tesera* (patch) frequently changing and the borders being periodically defined." Similarly, Borgias and Fonda (unpublished manuscript on the North Cascades) referred to the subalpine forests as a "fire etched mosaic." Daubenmire and Daubenmire (1968) wrote, "The vegetation (of the northern Rocky Mountains) consists mainly of a wide variety of intergrading, disturbance-induced communities . . ." Because the distribution of subalpine forests is patchy, the distribution of boreal owls in mountain ranges probably is patchy as well (Hayward *et al.* 1993) — possibly a significant contrast to the more continuous boreal forests of Canada. Understanding the processes related to the patchy nature of these forests is critical to management of the forest system and boreal owls.

The discontinuous distribution of the subalpine forests required by boreal owls can be attributed to several factors related to the probability of fire ignition and spread. In many areas, old subalpine forests develop only where fires are less frequent, e.g., on higher mountain slopes and along drainages (Franklin and Dyrness 1973, Romme and Knight 1981). Fuels remain moist for longer periods in both habitats, thereby reducing the probability of ignition. Also, valley bottoms are less likely to burn because fires usually move up drainage slopes rather than along valley bottoms. Similarly, higher mountain slopes with subalpine forests sometimes are appropriately viewed as isolated, topographic "islands." In such areas, a fairly small land area is subject to lightning strikes, and when a fire is started, it typically burns upward to treeline. Fire spread to other mountain peaks can occur through spotting, which adds further heterogeneity to the forest mosaic.

Notably, some mountains have comparatively flat plateaus that are high enough to provide the cool, subalpine environment apparently required by the boreal owl (e.g., the Middle Rocky Mountains; MacMahon and Anderson 1982). Owl habitat may be more uniformly distributed in such areas, but they also burn more uniformly and more frequently, thereby preventing the development of the old forests that the owls frequently use.

Another factor leading to discontinuity in owl habitat — possibly more discontinuity than for owls living at lower elevations — are the frequent meadows that interrupt subalpine forests. In general, these

meadows are caused by fine-textured geologic strata such as shales that are not favorable for tree establishment. Other meadows are found in low, comparatively flat depressions where herbaceous plants have become established and the soil often is too wet for upland conifers.

Forest fragmentation by clearcutting is another cause of habitat discontinuity. As described below, forest characteristics which result from clearcutting are not analagous to forests resulting from natural disturbance agents. Fragmentation of landscapes through clearcutting, then, may have different consequences for boreal owl populations than the pattern of fragmentation observed in unmanaged landscapes.

SUBALPINE FOREST DYNAMICS

Causes of Disturbance

Fire

Large-scale, stand-replacing fires are infrequent in the cool, moist subalpine forest environment, occurring only during exceptionally dry and windy summers. Such conditions occurred in the Greater Yellowstone Area in 1988. Extensive areas of old forest may burn under these conditions, presumably reducing the amount of boreal owl habitat; but such fires probably occur at fire-return intervals of 150 to >350 years (Arno 1980). When fires do occur, they do not burn uniformly so patches of old forest persist. Old forest conditions cannot develop in less than 150 years, so fires at more frequent intervals prevent old forest formation in subalpine forests. Characteristically, however, natural fires occur at longer intervals. Wind and insects are more frequent causes of disturbance than fire in many subalpine forests (Franklin 1988, Veblen *et al.* 1991a,b); disturbance by these agents typically increase the probability of fire.

Insects

The spruce beetle (*Dendroctonus rufipennis*) affects subalpine forests more than does any other insect (Schmid and Frye 1977, Baker and Veblen 1990, Veblen *et al.* 1991a,b). This insect is capable of killing a substantial proportion of the spruce overstory across thousands of hectares, and outbreaks occur throughout the range of Engelmann spruce (Schmid and Frye 1977). Outbreaks generally occur following disturbances such as blowdown, which increases beetle habitat and thereby stimulates beetle population growth.

The western spruce budworm (*Choristoneura occidentalis*) may be important locally in subalpine

forests, but it typically attacks Douglas-fir at lower elevations (Schweitzer *et al.* 1975, Brookes *et al.* 1987, Swetnam and Lynch 1989, Baker and Veblen 1990). Other insects such as pine sawflies (*Neodiprion spp.*), Engelmann spruce weevils (*Pissodes strobi*), and needle miners (*Taniva sp.*, *Coleopechnipes spp.*), kill individual trees or even small patches (McGregor and Quarles 1971). At lower elevations, the Douglas-fir tussock moth (*Orgyia pseudotsugata*), Douglas-fir beetle (*Dendroctonus pseudotsugae*), mountain pine beetle, and larch casebearers (*Coleophora laricella*) may also cause disturbance. Lodgepole pine can be killed by mountain pine beetles (*Dendroctonus ponderosae*) over large areas, but usually not in the subalpine zone because winter temperatures are too low for the beetle (Amman 1989).

The effects of insects on forest composition depend on various factors of which the following four are particularly salient: 1) the composition of the forest prior to the insect outbreak; 2) the relative susceptibility of the tree species to the insect involved; 3) the duration of the outbreak, which can be affected by climatic conditions; and 4) the landscape mosaic in which the outbreak occurs. Thus, a mountain pine beetle outbreak will have a minor effect on owls if comparatively few lodgepole pines grow in the stand, because spruce and fir are not susceptible to this insect. Only small canopy gaps would be created in this scenario. In other scenarios most of the trees could be killed, changing the forest structure dramatically.

The causes of insect outbreaks are still poorly understood. Generally, conifers produce sclerophyllous plant tissues that are resistant to attack and resins that are capable of blocking insect invasion. When stressed, however, whether by climatic conditions or competition from neighboring trees for water, nutrients, or light, their resistance is weakened. Outbreaks of both insects and diseases are then more likely to occur.

Disease

Pathogens appear to be a minor cause of disturbances in both subalpine and boreal forests (Elliott-Fisk 1988, Franklin 1988, Kaufmann *et al.* 1992). However, root rots (*Armillaria spp.* and *Phellinus wierii*) are commonly associated with subalpine forests and they can cause changes in forest structure (James *et al.* 1984, Matson and Boone 1984). Heart rots, canker diseases, and foliage diseases affect groups of trees locally, creating canopy gaps. Mistletoe (*Arceuthobium spp.*) affects forest structure over large areas, but more commonly in seral forests at elevations lower than where boreal owls occur.

Timber Harvesting

During the last century, timber harvesting has become an important disturbance in subalpine forests. Prior to this time, very few trees were harvested by humans (usually small ones to be used for fuel and poles). Large trees were first harvested in significant quantities in the mid- to late-1800's when immigrants from the east needed mine timbers and railroad ties. The market for sawtimber expanded rapidly during the following century and created a significant timber industry throughout the Rocky Mountains, Blue Mountains, and Northern Cascades. For various reasons, clearcutting was the preferred silvicultural system. Though different in several significant ways, both fire and clearcutting are stand-replacing disturbances. Selective harvesting, in contrast, leaves many live trees and is more analogous to some insect epidemics or wind storms.

The rotation age for harvesting subalpine forests typically ranges from 75-120 years. Forests cut at this frequency do not develop old forest characteristics such as abundant lichens and fungal sporocarps (important in the boreal owl food chain as food for red-backed voles). These characteristics likely require 150-200 years to develop. Furthermore, the application of a stand-replacement harvest at this frequency is quite different from natural disturbance regimes, which included frequent small-scale gap disturbances and a longer average stand replacement frequency. Currently, we do not know how long is required for the development of second-generation old forest following stand replacement harvests. Nowhere in western North America has this been accomplished. We also lack knowledge of differences in seral development following harvest versus natural disturbances. In particular, knowledge is lacking on the differences in detrital food webs, understory plants, and lichen populations. Typically, fires, insect epidemics, and wind storms leave large volumes of wood that, for millennia, have been incorporated into the soil. Timber harvesting removes a large proportion of that wood.

Contrasting Effects of Different Disturbances on Succession

Fire and clearcutting affect subalpine forests quite differently than do insects, pathogens, wind storms, and selective harvesting. Whereas stand-replacing disturbances kill both small and large trees, usually exposing the mineral soil for seedling establishment and initiating sec-

ondary succession, the other kinds of disturbances typically kill only the larger trees. They also add detritus to the forest floor and hasten the development of a multi-storied, uneven-aged climax forest; the understory vegetation is affected very little.

Various successional pathways for the development of spruce-fir forest following disturbances are possible, depending on the nature and intensity of disturbance, species composition prior to disturbance, soil and microclimatic characteristics, and climatic conditions after the disturbance (figure 1 from Stahelin 1943, see also Fischer and Clayton 1983 and Bradley *et al.* 1992b). Engelmann spruce, lodgepole pine, and sometimes aspen are the first dominants after stand-replacing fires in the Rocky Mountains (Brown 1975, Fischer and Clayton 1983, Crane and Fischer 1986, Fischer and Bradley 1987, Johnson and Fryer 1989, Veblen *et al.* 1991b, Bradley *et al.* 1992a). They may develop together or separately depending on moisture availability, seed availability, and, in the case of aspen, root systems that were not killed by the fire. In the northern Cascades, mountain hemlock and silver fir can be the pioneer species; but they persist in the climax forest along with subalpine fir that invades later (Franklin and Dyrness 1973). In the Rocky Mountains, subalpine fir becomes an important species after a century or more. Engelmann spruce persists during the entire successional sequence, but lodgepole pine becomes less common. The probability of developing an old-growth, uneven-aged forest increases with fire suppression and the relative moistness of the site (Day

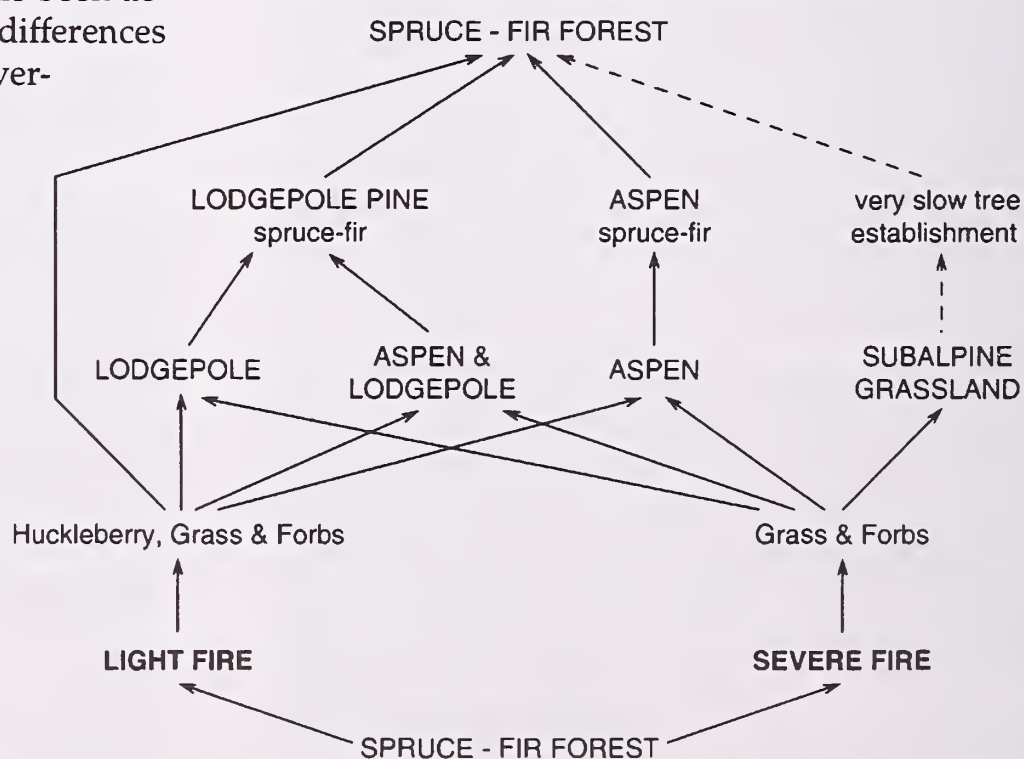


Figure 1. – Alternative successional patterns in central Rocky Mountain subalpine forests after light and severe fires (adapted from Stahelin 1943; see also Fischer and Clayton 1983, Fischer and Bradley 1987, Bradley *et al.* 1992a,b).

1972, Romme and Knight 1981). However, succession occurs slowly in the cold subalpine zone, often requiring 200 years or more. Rebertus *et al.* (1992) suggest that some important attributes of old forest may take substantially longer to develop, even on high quality sites. For example, density of large trees may take 500-700 years to peak, but a high density of large snags and logs takes even longer. Succession is equally slow in the Blue Mountains and northern Cascades.

After a forest is clearcut for the first time, succession of dominant trees proceeds similarly to that following a stand-replacing fire. Unlike the effects of fire, few dead trees remain after a clearcut. New tree establishment also might be slower without the bare mineral soil created by burning. Significantly, however, seedling establishment is often very slow at higher elevations after both burning and clearcutting (Alexander 1987). Conceivably, climatic conditions now are less favorable for seedling establishment than they were two or three centuries ago when the harvested forest became established. At high elevations it may not be possible for clearcut or burned forests to develop into the kind of old forests that boreal owls currently use. Now that may be possible only at lower elevations, and then only if rotation ages are long enough.

Tree establishment is less problematic lower in the subalpine zone, where both lodgepole pine and Engelmann spruce are well adapted as pioneer species. In particular, lodgepole pine often is the predominant seral species following a fire, especially when many of the trees have serotinous cones. These cones are produced during most years, but they remain closed for decades until opened by intense heat, such as during a fire. More than a million lodgepole seeds per hectare can be dispersed in a single year (Lotan 1975), often leading to the development of "doghair" stands. The growth of individual trees is slow in such dense stands, but the trees still produce new seed and they may survive for well over a century, though attaining less than 10 cm in diameter. Doghair stands have little understory growth to support the rodent populations preyed upon by owls. Conceivably, these dense stands could provide a barrier to owl movement.

While clearly an adaptation for fire, many of the serotinous cones with their enclosed seed could be burned during intense fires. The result would be fewer pine seedlings during the first few years. Lodgepole pine seedling density was found to be spatially variable three years after the Yellowstone fires of 1988, with the lowest densities in the middle of very hot burns and the highest densities near the edges of burns, where the fires were less intense and

where live trees persisted with unburned cones (Anderson and Romme 1991). Lodgepole pine density apparently is a function of fire intensity and seed mortality during fire as well as the percentage of trees that are serotinous. The development of old, second-generation forests probably takes longer after very hot fires.

Significantly, some lodgepole pines do not produce serotinous cones. The trait seems to be genetically determined, but it has at least three recognized phenotypes: closed cones that require temperatures of 45-60°C for opening, intermediate cones that require cooler temperatures (35-50°C), and non-serotinous cones that open at warm ambient temperatures of 25-50°C (Perry and Lotan 1977). All three phenotypes can be present in each stand, which helps explain why new seedlings emerge following disturbances other than fire. Muir and Lotan (1985a,b) observed that the proportions of the trees that are serotinous and non-serotinous depend on the nature of the last disturbance. Fires lead to a high proportion of the serotinous genotype because the heat opens the cones and an abundance of seed is dispersed when conditions for seedling establishment are ideal. However, non-serotinous trees are favored if the last disturbance was an insect epidemic or wind storm because most of the seed in serotinous cones is not dispersed; the primary seed source is from non-serotinous cones. Muir and Lotan (1985a) suggested that having both cone types present in a stand increases the chance of a species surviving any given kind of disturbance, and that management, both in wilderness and in timber production areas, should allow for both fire and non-fire disturbances so that a range of genotypes can be maintained. A significant element of biological diversity thereby endures.

Though lodgepole is clearly a seral species, some stands begin to develop multi-storied, old forest characteristics later in succession as the first generation of trees die, and as spruce, fir, and more lodgepole pine grow from the understory in gaps. The forest becomes uneven-aged, even with lodgepole pine in the overstory, and fallen logs become a prominent feature of the forest floor. Fungal sporocarps and other rodent food may become more abundant in the gaps than they were in the seral even-aged forest. Lichens could become more common also, though this probably depends on climatic conditions as well as successional stage (R. Rosentreter, pers. comm.).

The relative abundance of climax species varies greatly from place to place. In general, the largest and oldest trees in the Rocky Mountains are Engelmann spruce; the species may live 500 years or longer

(Oosting and Reed 1952, Shea 1985, Alexander 1987, Veblen *et al.* 1991b). Subalpine fir usually is more common, but the trees are smaller and younger, rarely more than 250 years old (Veblen 1986a,b, Peet 1988). Fir also produces 10-20 times more seedlings. Apparently, the new roots of fir seedlings are better able to penetrate the leaf, twig, and wood detritus that accumulates over the forest floor, while spruce seedlings usually emerge where mineral soil has become exposed, such as around the tipped root system of fallen trees. Some investigators also have observed spruce seedlings on rotting logs where the decomposing wood remains moist well into the summer (Lowdermilk 1925, McCullough 1948, Oosting and Reed 1952, Loope and Gruell 1973, Cui 1990). Spruce trees produce large amounts of seed every 2-5 years, subalpine fir about every 3 years (Alexander 1987).

Unlike the pines and Douglas fir, spruce and fir are capable of vegetative reproduction (layering) when lower branches are pressed to the ground by snow. The branch often develops adventitious roots, after which the end of the branch begins to grow upright into a new tree. Eventually, the branch connection to the parent tree decomposes. Clusters of subalpine fir often can be attributed to this cloning process.

The fact that subalpine fir reproduces more effectively (than Engelmann spruce) in the forest environment has led to speculation on how spruce persists as a co-dominant in the forest. Veblen (1986a) concluded that coexistence is possible because fir is shorter-lived but produces many seedlings, while Engelmann spruce compensates for poor reproductive success with increased longevity. Thus, the greater proportion of subalpine fir seedlings and saplings does not mean that it will eventually become the sole dominant.

It is tempting to view uneven-aged subalpine forests as being in a state of equilibrium. However, Aplet *et al.* (1988) studied several stands of spruce-fir-pine forest that spanned a 500-yr period (a chronosequence) and found that periodic disturbances cause continual changes in tree population structure. They hypothesized that, following a large scale disturbance such as a crown fire, all three species colonized the site together at the beginning of secondary succession. After 100-200 years, spruce could no longer reproduce in the forest understory, a period they labeled the "spruce exclusion phase." After another 100 years many dominant fir, spruce, and pine began to die, facilitating the "spruce reinitiation phase," during which canopy gaps appear and spruce (and perhaps lodgepole pine) are

again able to reproduce. The final phase they recognized was a "second generation spruce-fir forest" with considerable fuel accumulation. This phase would be very flammable during the next dry summer, but it would also support many fungi and a large lichen biomass. This may be a plausible successional sequence, but another crown fire could prevent the old spruce-fir forest from developing. As others have observed (Romme and Knight 1981, Johnson and Fryer 1989), the fire return interval may be short enough to ensure burning within the life span of the trees that invaded following the previous fire. Under such conditions, "old-growth" subalpine forests may never develop, although some characteristics of old forest may appear. As others have pointed out, however, many old spruce-fir stands classified as old growth may be transitional stands that are still primarily influenced by the original stand-replacing disturbance (Hayward 1991, Rebertus *et al.* 1992).

The stand development pattern described by Aplet *et al.* (1988) is undoubtedly influenced by insect outbreaks. As described previously, a common insect in spruce-fir forests is the spruce beetle, a bark beetle with a life cycle similar to the mountain pine beetle (Schmid and Hinds 1974, Alexander 1987, Baker and Veblen 1990, Veblen *et al.* 1991a). The spruce beetle attacks older stands with a high proportion of Engelmann spruce in the overstory. Usually, the susceptible stands have slow tree growth, suggesting that the trees are of low vigor. Abundant downed trees, whether due to logging or windthrow, may provide the energy base for initial development of the outbreak. The infestation opens the canopy, greatly accelerating the growth of the abundant, non-host subalpine fir plus spruce that are too small to be susceptible to attack. The growth of other plants is stimulated as well. The beetle thereby increases the proportion of the forest biomass in subalpine fir and other plants. Lodgepole pine and aspen may also become more common. Fuel biomass and continuity increase, which increases the probability of fire.

Unfortunately, most research on succession in western coniferous forests has focused on the trees. Much less is known about temporal changes in the abundance of lichens, fungal sporocarps, and non-arboreal understory plants such as grasses, forbs, and shrubs. Understory plant growth increases when competition for water, nutrients, and light diminishes following disturbances. Conversely, the understory biomass gradually declines as canopy gaps close. Gap formation can have dramatic local impacts on the understory. For example, a fallen tree

suddenly places an abundance of epiphytic lichens within reach of the small terrestrial mammals on which the boreal owl preys. Moreover, the death of individual trees can lead to an increase in fungal sporocarps (S. L. Miller, pers. comm.) and the growth of shrubs such as *Vaccinium scoparium* — other important food sources for small mammals. Thousands of years of wood production and slow decay in the cool subalpine environment have led to the detritus-based food web characteristic of old forests. The time required to reestablish such food webs after different kinds of stand-replacing disturbances is not known.

Small-scale disturbances in old forest apparently could improve boreal owl habitat by creating more snags in which woodpeckers can excavate cavities that boreal owls eventually occupy. Also, periodic tree mortality may reduce forest transpiration, at least for a time, which leaves more moisture in the soil to support the fungi and lichens that are important to the owl's prey. Forest gaps also may increase visibility, thereby improving prey capture. Many dead standing trees existed in pre-settlement subalpine forests, giving the forest a "salt-and-pepper" appearance (Baker and Veblen 1990). The forest today is more uniform due to timber harvesting that leaves fewer snags and to fire suppression that essentially has the potential of "homogenizing" the forest over large areas (Habeck and Mutch 1973). Simultaneously, the forests are being fragmented by clearcutting. As the participants of one recent workshop concluded (Kaufmann *et al.* 1992), forests and landscapes are being created that never existed previously. Can such "novel" forests serve as habitat for the boreal owl? What management practices should be implemented to maintain or create the kind of habitat required by the boreal owl and other species dependent on mature subalpine forests? Existing old forests surely will be affected by stand-replacing disturbances in the future. What kind of management is required to ensure that adequate owl habitat will be available where subalpine forests are isolated and often cover a small area? These questions are appropriate for forest planning in regions with subalpine forests.

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Conservation Status of Boreal Owls in the United States

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INTRODUCTION

Previous chapters outlined the biology and ecology of boreal owls as well as the ecology of important vegetation communities based on literature from North America and Europe. That technical review provides the basis to assess the current conservation status of boreal owls in the United States. By conservation status, we mean the demographic condition of the species as it relates to the likelihood of local and national persistence of wild populations over the long term. Are populations of boreal owls in the United States currently threatened? Are current land management practices likely to lead toward the peril of local or regional populations?

Like any scientific story, our understanding of boreal owl ecology is incomplete. In the face of incomplete knowledge, I will evaluate the status of boreal owls by asking a series of critical questions about the species and its habitat. My goal is to synthesize evidence necessary to build a case for one of the following conclusions: 1) populations of boreal owls in the United States are secure and will likely remain so given current land management practices; 2) populations of boreal owls are in peril (declining or experiencing some demographic trauma) or are likely to be in peril in the future given current land management practices; or 3) there is insufficient evidence to determine the species' conservation status.

Populations of boreal owls differ in biology and ecology depending on geographic setting (Korpimäki 1986, Hayward *et al.* 1993). Therefore, for this assessment, when answering the critical questions, I rely first on investigations from North America and use European studies to a lesser extent. A minimum of references are presented here as the literature was thoroughly reviewed in the previous chapters.

Is the Distribution and Abundance of the Boreal Owl Declining in All or Part of Its Range?

Distribution

The boreal owl is broadly distributed in North America, and its distribution likely has remained the same over the past few decades. The extensive geographic range of the species contributes toward species persistence.

During the past 15 years, numerous published reports have extended the recognized range of boreal owls in western North America. In 1980, the southern extent of the species' breeding range was thought to end in Canada. Today, evidence exists for breeding populations throughout the Rocky Mountains south to southwestern Colorado and northern New Mexico. Breeding boreal owls have also been documented in northern Minnesota. Do these records indicate an extension of the species' range?

The weight of evidence suggests that the actual distribution of boreal owls has not changed recently; rather, our knowledge of the species has changed radically. Several indirect lines of evidence support the contention that the extension of the species' recognized range stems from an increase in survey effort. First, historical records indicate that boreal owls were recorded in the western United States but not recognized as breeding. A close look at the literature indicates that boreal owls were documented as far south as Colorado for nearly 100 years (see Ryder *et al.* 1987). Historical records of boreal owls in Wyoming, Idaho, and Colorado were thought to represent nonbreeding "visitors." Despite the occurrence of boreal owls in the western United States, checklists and field guides did not list the species, even after breeding populations were documented in 1983.

Second, human use of boreal owl habitat has increased recently, raising the probability of documenting existing breeding populations. Winter recreation in high mountain lands has increased since the 1970's, bringing more people into boreal owl habi-

tats during the owls' most vocal period. Coincident with increased interest in winter sports (cross country and downhill skiing) has been an increase in roads in high mountain areas. Furthermore, biologists working with land management agencies have conducted surveys directed toward finding boreal owls. An increase in roads accessing high elevation forests and interest in the owl have facilitated location of breeding owls. In 1984 alone, during the first extensive surveys in the Northern Rocky Mountains, agency personnel found boreal owls on nine western national forests where the owl was not recognized previously.

Third, biologists in Europe have also located new populations of boreal owls and attributed these to increased interest in the species. Cramp (1977) describes extensions of the recognized range in Europe but does not believe the species has actually broadened its distribution.

Abundance

Local and regional trends in boreal owl abundance cannot be assessed with available data. Breeding populations of boreal owls were only recently documented throughout most of the species' range in the United States. In most cases, estimates of density or an index to abundance have not been made, precluding any assessments of trend in the near future. I am aware of only two populations (one in Idaho and one in Montana) that have been sampled using methods that will facilitate assessment of trend within the next 5 years (see Hayward *et al.* 1992).

Do Habitats Vary in Their Capacity to Support Boreal Owl Populations or to Support Particular Activities of the Owl? What Are the Important Characteristics of Those Habitats?

Study of boreal owl habitat use is limited. Investigators in Europe who have studied boreal owls for 2 decades have not focused on habitat use. In North America, only three studies have intensively examined habitat use. Despite this limited knowledge, the evidence supports the contention that boreal owls favor particular habitat characteristics at a variety of geographic scales. Consistently occupied habitat generally is mature or old spruce or spruce-fir forest.

The combined results of three, multiyear studies of boreal owls in North America indicate that boreal owls choose sites for nesting, roosting, and foraging nonrandomly (Bondrup-Nielsen 1978, Palmer 1986, and Hayward *et al.* 1993). Knowledge of habi-

tat use in North America stems largely from these studies. Studies from Europe corroborate the conclusion that boreal owls choose specific habitats at a variety of spatial scales. In general, habitat studies were observational, rather than experimental, and suffered from small sample sizes. Furthermore, none of the North American studies compared the relative fitness or productivity of individuals using various habitats. Despite these shortcomings (which are the norm in vertebrate ecology) these investigations were sound mensurative studies that showed boreal owls use habitats differentially for important life functions.

Regional

At the regional scale, knowledge of boreal owl distribution indicates particular habitat associations. Boreal owls occur only in subalpine forest habitats in the western United States (e.g., Hayward *et al.* 1993). Breeding populations have not been found more than 100 m below the spruce-fir zone in the Rocky Mountains. East of the Rocky Mountains, boreal owls do not occur south of boreal and transition boreal-temperate forests. These distributional boundaries suggest strong physiological, behavioral, or ecological barriers limiting the boreal owl. What characteristics of these forests are important in determining the broad distribution pattern of boreal owls is unknown but reasonable hypotheses were outlined in Chapters 9 and 10.

Landscape

At the landscape and home range scales, limited evidence indicates boreal owls use sites with particular forest characteristics (e.g., Sonerud 1986, Korpimäki 1988, Hayward *et al.* 1993). In both Europe and North America, quality foraging habitat is characterized as mature and older spruce or spruce-fir forest. During prey population declines in Finland, owl home ranges with a high proportion of spruce forest are consistently occupied while other ranges are only used during prey peaks. The regularly occupied home ranges also produce more fledglings than other sites, indicating a match between preferred habitat and productivity (Korpimäki 1988). In Idaho, nest sites of radio-marked owls occurred in the lowest elevation portion of home ranges (edge of elliptical home ranges) indicating the spatial segregation of habitats used for nesting vs. foraging and roosting (Hayward *et al.* 1993). Nest sites occurred in old aspen and old, mixed-conifer stands while roost and foraging sites were often in mature and older spruce-fir forest.

Microhabitat

At the microhabitat scale, boreal owls appear to use a nonrandom subset of sites for nesting, roosting, and foraging. The strength of evidence for habitat choice varies among investigations, each of which was conducted in a very different geographic setting. In some studies, selection was not demonstrated, while in others, used habitat was simply described.

Boreal owls are obligate cavity nesters. One study suggests that boreal owls select among available nest sites when a range of sites is available. In an experimental study in Idaho, suitable nest sites in lodgepole pine forest were not used when alternates were available in the old mixed-conifer forest (Hayward *et al.* 1993). In the same study, an analysis comparing 28 nest sites and 101 random sites indicated the owls used forests with multiple canopy layers, large diameter trees, and high basal area.

Although boreal owls have been shown to choose particular forest habitats for nesting, the species will accept a broad range of nest sites. Simple descriptive studies demonstrate this range. Nests have been found almost exclusively in aspen in Canada and Minnesota, in spruce and lodgepole in Colorado, and lodgepole and spruce-fir forest in Montana. Nest boxes placed in clearcuts in Idaho and Sweden have been used. In these cases, spruce or spruce-fir forest occurred nearby.

The importance of specific roosting habitat seems to vary depending upon the threat of predation and degree of thermal stress. In Canada, owls did not select particular sites for roosting. In Idaho, boreal owls exhibited symptoms of summer heat stress and were shown to choose cool microsites for roosting. Mature and old spruce-fir forest was chosen for summer roosts. These stands had higher basal areas, higher crown closures, and higher tree densities than random sites. During winter, these same owls were less selective in roost choice.

Microhabitat characteristics of boreal owl foraging habitat have not been studied. Therefore, despite evidence for foraging habitat choice at broader scales, the microhabitat characteristics of quality foraging habitat have not been identified.

Do Habitats Vary in Their Capacity to Support Principal Prey Species?

Primary prey of boreal owls in North America include red-backed voles (*Clethrionomys* spp.), field voles (*Microtus* spp.), deer mice, shrews, flying squirrels (*Glaucomys sabrinus*), and pocket gophers (*Thomomys talpoides*). Most important among these

are red-backed voles and field voles, both of which occur in specific habitats. In the western United States and Canada, red-backed voles are most abundant in old spruce-fir forests and rarely occur in unforested habitats. Major foods of red-backed voles in the western United States are scarce in young forest stands. In contrast, red-backed voles in the eastern United States occur in a variety of forest age classes but (similar to western areas) are most common in mesic forest. Field voles rarely occur in forest stands and are most abundant in mesic meadows. Forest management practices significantly influence the abundance of these and other small mammal prey species (Campbell and Clark 1980, Ramirez and Hornocker 1981, Halvorson 1982, Scrivner and Smith 1984). Although the outcome of particular management practices is poorly understood, stand replacement treatments (e.g., clear cut harvests) lead to the most dramatic changes.

If the Boreal Owl or Its Prey Select Particular Habitats, Are These Habitats Declining or Being Stressed by Current Management?

Studies from a few geographic areas indicate boreal owls and their prey demonstrate selection for particular habitats. The paucity of research on this owl and its prey makes the geographic extent of this pattern unclear. Furthermore, the characteristics of high quality habitat for the owl's prey are not known sufficiently to set management guidelines.

The available evidence (see Chapter 9 concerning nesting, roosting, and foraging habitat) does suggest that mature and older forest in the spruce-fir zone provides the highest quality habitat for boreal owls and their prey. These forests occur as the upper forested zone on mountains in the western United States. As such, if global climate change shifts life-zones upward in elevation (as is predicted to happen), these habitats will decline (see Chapter 10).

Climate change portends consequences beyond a potential future change in the elevation of life zones. The mature and older forests used by boreal owls today became established centuries ago, under different climatic circumstances. As pointed out by Knight (Chapter 10), "Conceivably, climatic conditions now are less favorable for seedling establishment than they were two or three centuries ago, when the harvested forest became established. At high elevations it may not be possible to count on clearcut or burned forests eventually growing back to the kind of old forests that boreal owls currently use." If timber harvest and other land management

practices are accelerating the rate of stand replacement and changing the distribution of forest age classes, the abundance of old forest stands may be declining faster than under a natural disturbance regime dominated by gap forming disturbance such as disease and blowdown.

Compared to recent historic times, old spruce-fir forests are likely less abundant (Chapter 10). While fire suppression has promoted an increase in older successional stages, timber harvest, using even-aged methods, has reduced the area of old forest. A long-term consequence of fire suppression, however, is fuel build-up that may lead to larger, more intensive fires, ultimately reducing the area of old forest. Overall, in the western United States, where most is known of boreal owl biology, the area of high quality habitat is likely declining and will continue to decline as forest management is carried out as currently outlined in forest plans. A review of 14 National Forest plans from Regions 1 and 4 indicated a reluctance to initiate uneven-aged management in many spruce-fir stands (Hayward *et al.* 1993). Our interpretation of 14 plans in 1989 indicated even-aged management would dominate on all but one forest.

The quality of habitats used by the owls and primary prey is likely declining as well as the area. Alexander (1987) indicated that spruce now leads all species except ponderosa pine in annual volume cut in the central and southern Rocky Mountains. Current knowledge is not sufficient to quantify the rate or extent of habitat decline. Patterns of subalpine forest dynamics described in Chapter 10 indicate some potential consequences of timber harvest dominated by large clearcuts. While insects and wind were the most frequent disturbance agents in subalpine forests prior to European settlement, the effects of clearcuts are similar to fire, which was a less common disturbance agent. Tree mortality due to insects and wind lead to gap processes that support the boreal owl food web. Natural disturbance patterns also resulted in a more heterogeneous forest than occurs with prolonged fire suppression and clearcut harvesting. The mosaic forest would support a variety of small mammal species and abundant red-backed voles (Chapter 9). The loss of large snags and large downed logs associated with standard forest practices likely lowers habitat quality for the owl and its prey. Forest practices that reduce arboreal lichen, particularly *Bryoria* spp., also likely reduce habitat quality.

Do the Life History and Ecology of the Boreal Owl Suggest That Populations Are Vulnerable to Habitat Change?

Cavity Nesting

Boreal owls require large tree cavities or artificial nest structures to breed. This is the most obvious habitat requirement of the species and one that has important consequences. Unless artificial structures are provided, boreal owls will not persist in landscapes where trees are too small to produce the large cavities required by the owl or where primary cavity excavators are missing. Natural tree cavities (produced by branch loss or other breakage) are used occasionally by boreal owls but unlikely to be common enough to support a population of owls. Rotations of 70-120 years will not produce the size class of trees necessary for natural nest sites.

Information is not available indicating in what geographic areas boreal owls may be cavity limited. Owl populations in regions south of the breeding range for pileated woodpeckers (*Dryocopus pileatus*) are more likely candidates for cavity limitation.

Changes in cavity availability have likely occurred during the past century due to forest management. The extent of these changes and their consequences have not been documented. Timber harvest prescriptions that removed all trees, or all large trees and snags, have eliminated existing cavities and precluded new cavities on the site for up to two centuries depending on tree growth. Harvest rotations that prevent the development of snags >38 cm dbh permanently preclude nesting from the site. In contrast to the consequences of timber management, in the short term fire suppression has likely increased the availability of large cavities by reducing the loss of old forest through fire. The long-term consequence may be different, however, if fire suppression leads to larger, higher intensity fires that burn stands on mesic and moist microsites that were less likely to burn under the natural fire regime.

Changes in forest conditions that lead to reductions in large diameter snags or large live trees with heart-rot will lead to cavity limitation. Similar consequences will occur with changes that reduce habitat quality for primary cavity nesters.

Productivity

Boreal owls in the western United States exhibit variable year-to-year productivity and appear to have relatively low average clutch sizes. These factors have been associated with decreased probabilities of population persistence (Goodman 1987, Pimm, *et al.* 1988). Variable productivity in boreal

owls stems largely from year-to-year variation in available prey. In Europe, extreme variation in the number of breeding pairs and clutch size have been documented. In North America few investigators have documented productivity over multiple years but variation due to changing prey populations has been reported. Variation in winter and spring weather may also lead to variation in productivity. Small, isolated populations of owls would be most susceptible to a series of years with extremely low reproduction.

The average and maximum productivity of boreal owls recorded in the western United States are much lower than records from Europe. This suggests that populations studied in the United States may produce fewer surplus individuals even in good breeding years. The ability of source populations to supplement less productive populations therefore may be less than in Europe. Our understanding of the comparative demography of boreal owls is not sufficient to assess the influence of productivity on the relative stability of various populations.

The degree to which productivity is density dependent, especially at low population densities, is important in assessing boreal owl demography. We do not know to what extent productivity is density dependent or whether boreal owls are likely to experience an Allee effect (Allee 1931) at modest population sizes. A strong Allee effect could result if boreal owls experience difficulty in locating mates at low population densities.

Survival

Limited information on boreal owl annual survival gives an unclear picture of the impact this life history parameter may have on population growth. The few estimates of adult and juvenile survival have potential for bias and are imprecise. Estimates range from about 45 to 80% adult survival and 20-50% for juveniles. Both year-to-year variability and average survival rates are important in assessing the status of boreal owl demography. Furthermore, the degree of inverse density dependence in this parameter is important. Neither is known for any population. In populations where average survival is high and not variable, concern over low relative productivity is reduced. Low survival rates, however, would lead to greater concern over the relatively low clutch sizes recorded in the western United States.

The environment occupied by boreal owls is variable and harsh. Therefore, the probability for catastrophic events leading to increased mortality may be high. The nomadic nature of boreal owls is a testament to this variability (Andersson 1980). During

periods of environmental stress, boreal owls move to new locations. These movements could contribute to periodic extinction within local habitats. It is unknown, however, whether nomadism increases or decreases persistence among linked small populations.

Home Range Size

Home range sizes of boreal owls in the western United States are large; winter and summer ranges both average over 1,000 ha and home ranges as large as 3,390 ha have been estimated. These areas are large for a medium size predator. Boreal owl home ranges are comparable to those used by the much larger spotted owl (*Strix occidentalis*). Whether large ranges are the norm for the species in the United States is unknown.

Several factors likely contribute to large boreal owl home ranges. In some regions, no single vegetation type provides optimum nesting, roosting, and foraging habitat, and these vegetation types are geographically disjunct. Therefore, geographic features may lead to a broad dispersion of resources, forcing the owls to move long distances to fulfill life requirements. In addition, low productivity of small mammals may also contribute to large owl ranges. Lindstedt *et al.* (1986) showed that home range size among carnivores is related to prey production.

In any case, large home ranges lead to high energy expenditure during daily movements. Boreal owls in some areas appear to need large areas to meet seasonal needs. Hirons (1985) has shown that, at least for the tawny owl (*Strix aluco*), clutch size is limited by energy available to the female prior to laying. The large home ranges and low clutch sizes observed in boreal owls in the western United States seem to fit this pattern.

The use of large home ranges by boreal owls is a conservation concern for two reasons. Populations of individuals requiring large ranges may be energetically stressed and less resilient to further stress. Also, land management must provide habitat within large areas to meet individual as well as population needs.

Trophic Position

Boreal owls are likely the most important avian predator of small mammals in subalpine forests in the western United States. As such, they rely on the integrity of 2-3 trophic levels. As described in Chapter 9, the boreal owl's food web in subalpine forests is linked strongly to the detritus system and involves many direct and indirect linkages among trees, insects, pathogens, fungi, and vertebrates. This sys-

tem appears to support larger prey biomass in older forests (Hayward *et al.* 1993). The food web is poorly understood but the boreal owl certainly occupies a top trophic position. The probability for persistence of species at higher trophic levels is thought to be less than for primary producers or primary consumers.

Metapopulation Structure

Boreal owls in western North America occur in relatively small, semi-isolated populations (see figure 1 in Chapter 9) and therefore, individual populations are vulnerable to extinction due to demographic and environmental stochasticity (Pimm *et al.* 1988). Therefore, the natural distribution pattern of the species south of the boreal forest places individual populations at risk due to their relative small size. Why is this the case?

Boreal owls are the only Strigiform in the western United States that occurs almost exclusively in subalpine forest. Because these forests occur only in high mountain areas, populations exist in patches limited by the extent of subalpine forest, separated from other patches by montane forest and nonforested habitats (see figure 1, Chapter 9 for an example). For example, within USDA Forest Service Region 1, ~9% of the forested land supports spruce-fir forest 15 cm dbh or larger (J. W. Laux, pers. comm.). On seven forests in Idaho south of the Salmon River, spruce-fir forest covers ~7% of the forested landscape (H. A. Cheatham, pers. commun.). These figures demonstrate the limited extent of boreal owl populations despite their broad geographic range. Demographic linkage among patches likely depends on long-distance juvenile dispersal and adult emigration. The nomadic nature of boreal owls should facilitate this linkage. The degree of connectivity, characteristics of the demographic relationships, and processes that control the connectivity, however, are not known.

Small isolated populations of any organism are expected to experience lower persistence probabilities than larger or more linked populations (MacArthur and Wilson 1967, Pimm *et al.* 1988). This is hypothesized to occur for several reasons. Small populations may drift to extinction due to random demographic events (demographic stochasticity; e.g., Shaffer 1981). Similarly, an environmental catastrophe affecting a relatively small area (e.g., stand replacement fire) is more likely to influence a large proportion of individuals in a small, rather than large, population. Isolated populations are also less likely to experience demographic rescue than connected groups (Brown and Kodric-Brown 1977). Therefore, compared to other owl species, individual

boreal owl populations may have lower persistence probabilities due specifically to natural distribution patterns.

Any environmental change that reduces the average size of habitat islands occupied by boreal owls is likely to decrease the probability of population persistence in the larger boreal owl metapopulation. An increase in fire frequency in subalpine forests, or reduction in forest area through timber harvest, could lead to reduced habitat area. Our understanding of owl-habitat and prey-habitat relationships is not sufficient to adequately predict what range of habitat alterations (e.g., silvicultural prescriptions) lead to reduced habitat area; however, short rotation, even-age management will clearly be detrimental. We also do not understand how large boreal owl populations must be before stochastic events become less of a concern.

Similarly, environmental change that reduces the linkage among populations is likely to decrease the probability of population persistence in the larger boreal owl metapopulation (due to demographic and genetic problems). Habitat conditions in the matrix surrounding occupied owl habitat will influence the probability of successful dispersal among populations. Furthermore, the productivity of individual populations will influence the number of individuals dispersing to other groups. What factors control successful dispersal and how those factors interact, however, is unknown.

WHAT IS THE CURRENT AND PROJECTED CONSERVATION STATUS OF THE BOREAL OWL?

The current conservation status of boreal owls is unknown. Knowledge of the species in North America is far from sufficient to adequately assess the species' status. Fifteen years ago, the owl was not recognized as a breeding resident of the lower 48 states. To date, only three studies have examined the species' habitat and/or demography; each of these were small, short-term investigations. Based on existing information, however, I tentatively conclude that except in local situations, boreal owls are currently secure but are likely to be in peril in the future given current land management practices. Therefore, I suggest that a conservation strategy is needed for boreal owls. These conclusions are based on the following points.

- Boreal owls currently are well distributed across a large geographic range and therefore the species is not in any immediate peril in the United States or worldwide. Furthermore, based on the only two

populations where nest occupancy and productivity is being monitored in the United States, nest occupancy and productivity are remaining constant.

- Populations of boreal owls in Fennoscandia have persisted and appear to be demographically vigorous despite human disturbance and a long history of forest management. These populations rely on artificial nest structures and exist in a very different ecological setting (boreal forest) than most populations in the United States. Still, the persistence of these populations suggests that, with proper forest management, boreal owls can co-occur with resource development including timber harvest. This statement must not be taken to indicate that all populations of boreal owls will respond similarly to environmental change. Boreal owls use habitat differently and have different demographic characteristics, throughout their range. Therefore, the response to forest management must be expected to differ in different ecological settings. Populations in the southern portion of the species' range have lower productivity and appear to use old forest habitats that are declining in aerial extent.

- In productive forest habitats, boreal owls have a high potential rate of population growth based on their dramatic numeric and functional response to changing prey populations. Therefore, populations can recover following declines if habitat is intact and prey are abundant.

- Conservation concerns for boreal owls arise when one considers long term persistence and/or focuses on individual populations. These concerns are based on the available information on boreal owl habitat use, the dynamics of those habitats, trends in forest management, and the species' life history. Specifically:

- The available data indicate that boreal owls, in at least some populations in the United States, use mature and older forest for foraging, roosting, and nesting. Primary prey of boreal owls also are more abundant in mature and older forests. The relative abundance of mature and older forest declines under traditional forest management programs as demonstrated in the Pacific Northwest and Northern Rockies. Therefore, habitat that provides necessary life requisites (food, thermal cover, and nesting substrate) has been declining and will continue to do so under current management plans, jeopardizing the long-term persistence of boreal owls in the United States.

- Habitats used by boreal owls develop slowly after deforestation due to the short growing season in subalpine environments. Therefore, forest stands may require several centuries to become

quality foraging or nesting habitat after stand removal; recovery of degraded habitat will be an extremely long-term process. As outlined in National Forest plans, clearcutting is the dominant management direction in subalpine forests in the northern Rockies. Development of mature and old forest from this management is questionable and, to date, has not been observed (see Chapter 10). If timber harvest decreases in the Pacific Northwest and shifts to the northern Rockies the threat to boreal owl habitat will increase.

- Populations of boreal owls studied in the western United States are less productive than most of those documented in Europe. Further reductions in productivity due to declines in habitat quality will reduce the average persistence time for populations.

- Individual populations of boreal owls in the United States are relatively small and dispersed due to the naturally patchy distribution of subalpine and boreal forest habitats. The populations have lower individual persistence probabilities than would larger populations. The persistence of individual populations, then, will be influenced by relatively small land management activities.

- Because of the high temporal variability in boreal owl productivity and the nomadic nature of the species, persistence of individual populations may rely heavily on neighboring populations. Due to this metapopulation structure, the persistence of individual populations and (potentially) large segments of the metapopulation could rest on particular key populations that provide surplus dispersing individuals or act as stepping stones for exchange among populations. The identity or even existence of such key populations is unknown and therefore their protection is not assured.

- Land management in the matrix of habitat surrounding subalpine forests will influence the success of dispersing owls. Therefore management outside the species' primary habitat will have consequences for the owl.

WHAT ARE THE MANAGEMENT CONSIDERATIONS?

A thorough discussion of management considerations of this assessment would be largely redundant with previous sections. A brief outline of the most relevant considerations follows.

Boreal owls occupy forest habitat. The future condition of forest structure will influence populations of this avian carnivore. The link between forest structure and composition and the status of boreal owl

populations is strong but indirect. Forest structure influences the availability of suitable cavities, the quality of roost sites, the foraging movements of individual owls, and prey availability. Landscapes without forest cannot support boreal owls; in forested lands, forest structure influences owl population status. Management of forest structure from the stand to landscape scale in subalpine and boreal to boreal-transition forest, then, will influence the long-term conservation status of this species. Because forest succession is slow in spruce-fir and boreal forests, management must acknowledge that clearcut sites will remain unsuitable for roosting or foraging for a century or more and new nest trees will not develop in some situations for two centuries or longer. Scientific understanding of boreal owl habitat relationships has not advanced sufficiently to devise sophisticated habitat management guidelines for any region. It is clear, however, that large clearcuts eliminate boreal owl habitat for many years and that clearcutting does not mimic the dominant natural disturbance agents in this system. Modification of these forests in ways that remove characteristics of mature and old forests should be done with caution. Monitoring the consequences of forest change at the stand and broader scales will be important in improving management (i.e., adaptive management involving researchers and managers).

Management of forest structure for any single life requisite (nesting, roosting, or foraging) will not assure suitable habitat to conserve boreal owl populations. Therefore, management should not be framed in terms of "management for nesting habitat" or another life requisite. Instead, management for boreal owls will be most successful if placed in an ecosystem context. The boreal owl depends on a plethora of other forest organisms: primary cavity nesters, small mammals, fungi, lichen, insects, and the dominant forest trees to name just a few (see figure 5, Chapter 9). Therefore, boreal owl management is a component of ecosystem management in subalpine forests in the western United States and boreal/boreal-transition forests in the east.

Conservation of boreal owls will require a regional approach to habitat management. Because populations of boreal owls in the United States likely occur in a complex metapopulation structure, the status of any single population is determined in part by many other populations. Management of individual populations outside the context of the larger metapopulation ignores the fact that most boreal owl populations are small and therefore have low probability of persistence in isolation. Even if high quality habitat remains within any small owl population,

the population is likely to become extinct without dispersal from other groups. Identification and maintenance of source populations within a region will be a key to boreal owl management.

Finally, the knowledge necessary to build a conservation strategy is lacking and without a conservation strategy, persistence of this owl over the long term is questionable. Many key aspects of boreal owl demography, habitat use, and the owl's relationship with the forest system (primary cavity nesters, prey, predators, etc.) have not been investigated for any population. Most of the links represented in figure 5 (Chapter 9) are inferred and not backed by direct empirical information. Much of what we do know results from investigations in Europe. How this knowledge relates to particular populations in North America is unknown. Therefore, anything but the most general analysis of management impacts will not be possible without further knowledge.

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Information Needs: Boreal Owls

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INTRODUCTION

Most humans are reluctant to make decisions without thorough knowledge of the consequences of those decisions. Therefore, a desire for further research is almost universal in any complex management arena. The value of further study is determined, in part, by the cost in time and resources to obtain new information and the cost of making incorrect decisions without the desired knowledge. In the case of managing forest lands and conserving boreal owls, our knowledge is so limited that well directed research on distribution, habitat use at many scales linked with studies of local demography, forest history, and interactions with competitors and predators can further our understanding at little expense compared to the potential benefits of managing forests without adverse effects on boreal owls and the larger subalpine ecosystem.

In this chapter, I will assess the strength of existing knowledge in forming a conservation strategy. Then I will discuss some strategies for obtaining needed information. This chapter will include few citations because it relies on Chapters 9 and 10 which review literature on this species and some of the forests it inhabits.

STRENGTH OF EXISTING KNOWLEDGE TO FORMULATE A CONSERVATION STRATEGY

Throughout this section I approached each topic as a question. Is our understanding of this topic sufficient to support the development of a sound, national-scale conservation strategy for the boreal owl? For example, "is the response of boreal owls to stand level habitat change understood in sufficient detail to formulate a conservation strategy?"

Distribution

Current knowledge of boreal owl distribution is not sufficient to support the development of con-

servation strategies. In the western United States (excluding Alaska), our knowledge is sufficient to predict, on a broad scale, where boreal owls are likely to occur and thereby indicate to land managers where management of the species should be a concern (see Map 2). In Alaska and east of the Rocky Mountains, particularly in the Great Lakes region and New England, understanding of the species distributional status is very weak. Knowledge of distribution is growing rapidly, however, and land management agencies have the capability to obtain the necessary information in several years. Methods for determining boreal owl distribution (not abundance) using playback surveys have been developed and are being used by managers.

Response of Boreal Owls to Stand-Level Habitat Changes

Current knowledge indicates that boreal owls in some geographic areas use mature and older forest habitats for critical life functions. Land managers, however, must predict the response of particular boreal owl populations to various management actions in order to assess the consequences of alternatives. Our knowledge is not sufficient to complete this task.

Our understanding of habitat use by boreal owls does not allow a ranking of habitats in terms of quality. Knowledge of habitat use based solely upon observations of habitat use will not be sufficient to guide habitat management. Rather, the relative productivity of owl populations among different habitats must be discerned in order to provide a ranking system with which to weigh alternative land management schemes.

Even habitat use data are unavailable for most geographic areas within the species' range. Geographic variation in habitat quality must be documented and developed into a ranking among habitats. Furthermore, proximate and ultimate factors determining the observed pattern of owl success among habitats must be understood in order to pre-

dict habitat use patterns for locales other than those studied. In other words, the relationship between the owl and its prey, primary cavity nesters, potential predators, and competitors and habitat relationships of each must be addressed to formulate a predictive model useful in evaluating management alternatives.

Effects of Landscape-Scale Changes on Home Range Use

Boreal owl studies have not examined the influence of habitat characteristics at the landscape scale on home range size or the success of individuals. The literature demonstrates that under some circumstances boreal owls occupy home ranges that exceed 2,000 ha and therefore indicates that management for boreal owls must consider extensive landscapes. The available studies do not aid managers in evaluating different mixes of forest age classes or provide a sound basis for predicting local or regional variation in home range use.

Effects of Regional-Scale Habitat Changes on Movement Patterns

Annual and seasonal movement patterns of boreal owls in North America are virtually unknown. Without this knowledge the demographic interactions among populations forming the larger metapopulation cannot be discerned. Therefore, the regional effects of local management actions cannot be addressed. For example, current knowledge of owl movements is not sufficient to determine whether management in montane forests below the subalpine zone will influence movements between populations.

Effects of Stand-Level Habitat Changes on Foraging Behavior

Boreal owl foraging behavior and habitat use is very poorly understood. For instance, the response of foraging owls to landscape boundaries (meadow or clearcut edges, changes in tree density) have not been observed. The interaction between prey abundance and habitat structure in determining prey availability is also poorly understood. The importance of understanding the foraging ecology of boreal owls cannot be over emphasized. Studies in Europe and North America indicate populations are frequently food limited. Prey abundance and foraging habitat condition together determine population trend for many populations.

Understanding how owl movements change when individuals encounter landscape boundaries of different types and the role of corridors in dispersal will facilitate building models to predict the impact of different harvest prescriptions on foraging success. Coordinated investigations examining the relationship between habitat condition and prey abundance would increase the predictive power of such a model.

Demography

Knowledge of boreal owl demography is not sufficient to estimate persistence of either local populations or metapopulations. Reproductive rates of boreal owls and the factors determining productivity are documented for populations in Europe, and productivity has been observed for several populations in North America. Age-specific survival and factors influencing survival are virtually unknown. Likewise, age-specific dispersal and the factors influencing immigration and emigration are not understood. The interaction between environmental conditions (forest structure, prey populations, predators, competitors, landscape patterns) and demographic parameters must be understood prior to developing comprehensive management plans for boreal owls. This does not mean that management is not possible without data on the demography of every target population. Rather, patterns of change in demography across the species' range should be understood so that a reductionist approach to management is unnecessary.

Methods to monitor the trend of boreal owls in selected populations will be necessary to evaluate management practices and facilitate adaptive management responses. Development of methods other than playback surveys has begun (Hayward *et al.* 1992) but these methods must be validated and refined if they are to be used effectively by management.

Dynamics of Primary Plant Communities

Knowledge of the successional dynamics of subalpine and boreal forests, while not complete, is extensive and will facilitate prediction of future forest conditions, particularly as that knowledge relates to the dominant tree species. Forest ecologists understand many of the factors related to the occurrence of major natural disturbance agents (fire, insects, windfall, and disease). Factors influencing seed crops, regeneration and survival of trees, gap dynamics, and material cycling have been studied. The

stochastic nature of disturbance agents have been incorporated into conceptual models of forest dynamics at the stand and landscape scale.

Understanding of the dynamics of forest species other than the dominant tree species is less complete. The seral development of the detritus system, so important to subalpine forests, is not understood. Similarly, the dynamics of fungi and lichen populations that are important to small mammals have received little attention. Knowledge of understory-plant population dynamics is incomplete. These areas of forest ecology need further attention in order to understand the dynamics of small mammal populations.

The population dynamics (production, survival) of tree cavities used by boreal owls is also poorly understood. Biologists do not understand the characteristics of forest stands (other than tree size and presence of primary cavity excavators) that determine the production of tree cavities. The role of tree disease (fungi, insects), wind damage, and moisture conditions in cavity production are not understood. Likewise, what factors determine the lifespan of tree cavities has received limited attention.

History of Distribution and Composition of Forest Communities

Forest ecology has recently directed more attention toward the historical ecology of forests. Despite these efforts, synthesis of data on the historic abundance and distribution of subalpine and boreal forests is not sufficient to indicate how current trends compare to the past. In particular, knowledge of patterns in distribution and abundance of older age classes of these forests has not been synthesized.

To aid in conservation planning for boreal owls, historic ecology must include investigations examining patterns in these forests thousands of years ago as well as in recent centuries. The value of the historic information lies in the perspective it can provide on the potential variation in boreal owl distribution in the past and therefore the range of conditions that the species faced.

A RESEARCH DIRECTION

The assessment of current knowledge points to major topics that must be addressed in future research designed to provide the basis for a conservation strategy. I will not set priorities among these themes because many of the topics are parallel. For instance, knowledge necessary to rank habitat quality will not improve habitat management without

knowledge of forest dynamics. Instead, in the section that follows, I provide direction in research philosophy and ideas for research approaches. My goal is to outline the scope of investigative approaches that will be necessary to obtain the knowledge highlighted above.

Integrate a Variety of Research Tools

A research program designed to obtain the knowledge necessary to build a conservation strategy for boreal owls will require the integration of several research approaches. Modeling, field experiments, and observational studies must be integrated so the knowledge stemming from each approach contributes toward corroborating or refuting key hypotheses. It will be necessary to coordinate efforts using each of these tools in several strategically selected geographic locales in order to elucidate the ecology of boreal owls in particular environmental settings and describe how the species' ecology varies across environmental gradients. In addition to employing a range of research approaches, studies must be carried out across a range of spatial scales. Below I will describe how I envision the employment of these research tools to obtain the information necessary to manage boreal owls over a broad geographic area.

Modeling

Boreal Owls in the Subalpine Forest.—The biological and ecological topics identified in the first portion of this chapter represent interesting research topics on their own but become significant when integrated as a body of knowledge to understand the subalpine forest system in which the boreal owl exists. The envirogram depicted in figure 5, Chapter 9 represents a hypothesis of how the components of the subalpine forest relate to the ecology of boreal owls. This envirogram should be elaborated into a model describing the processes that link the boreal owl to other components of the subalpine forest system. The model should predict how changes in subalpine forests (e.g., biomass of logs, abundance of woodpeckers, or size class distribution of trees) would impact boreal owl populations. Such a model would begin as a qualitative representation of the system generating specific hypotheses that could be tested through field research. As particular linkages are examined, portions of the model should be refined into quantitative expressions of the system. Without such a predictive model, research at the stand and watershed scales will lack focus and likely not concentrate on key characteristics of the owl/forest system. A well developed and tested model

would ultimately provide managers with a tool to evaluate the consequences of management on the boreal owl through the impacts on the forest system.

Individual-Population Demographic Models.—Although reliable estimates of mortality rates, immigration rates, and emigration rates are not available, preliminary modeling of boreal owl demography will be useful in focusing research and refining the assessment of conservation status. Preliminary estimates of demographic parameters (which are available — see Chapter 9) would permit examination of life history sensitivities. Based on these analyses, and refinements of the models as more precise demographic data are gathered, managers will become aware of aspects of the owl's life history that are more sensitive to change. Through use of these demographic models, assessments of persistence probabilities will be refined and management alternatives more easily compared.

Examination of individual-population demographic models would aid in understanding the relative quality of different habitats for boreal owls. Habitat quality is most directly expressed through population trend (quality habitat leading to $\lambda > 1$). Through the joint examination of local demography and habitat characteristics, poor and good quality habitat may be identified, providing important information for managers (see Small Scale Demography below).

Spatially Explicit Metapopulation Models.—Based on the distribution and life history of boreal owls, Hayward *et al.* (1993) hypothesized that boreal owls occur in the United States as a strongly structured metapopulation. This hypothesis must be tested using observational field studies documenting the degree of demographic linkage among boreal owls occupying separate patches of habitat. Based on this hypothesis, a metapopulation model for the Rocky Mountains, Blue Mountains, and Northern Cascades should be built. This model would integrate with field studies on boreal owl dispersal, local demography, and habitat use in an interactive sense. Field results would be used to parameterize the model while the model would be employed to focus field studies geographically and toward particular questions. The model would be tested and refined as field data accumulated.

The Geographic Information Systems (GIS) data base necessary to develop such a model would be expensive and time consuming to develop. However, the U.S. Fish and Wildlife Service's Gap Analysis program could provide the necessary data at the proper scale. Using the vegetation and topographic

layers built into the Gap data bases, the predicted distribution of boreal owl populations would be estimated based on a series of geographically tuned owl habitat models.

The metapopulation model would be a valuable tool for management and research. Managers could immediately employ the geographic data in biological evaluations or other impact assessments. They could also use the model to predict the location of unidentified owl populations and test those predictions through surveys. Research would use the model to aid in setting priorities among research topics based on a sensitivity analysis. The model could also aid in choosing study areas based on which owl populations are predicted to be key populations for the persistence of boreal owls.

Experimental Studies Using Management Treatments

Experimentation is the workhorse of modern science. Experiments provide the most straight-forward methods to examine cause-and-effect and to determine the processes responsible for patterns observed in natural history investigations. Unfortunately, ecological experiments employing appropriate sampling designs and proper controls are difficult to design and execute (Hairston 1989), especially in studies of large, low density, mobile vertebrates. Coordinated efforts between management and research can overcome some of the logistic difficulties in producing large scale treatments and measuring the effects.

Experiments will be necessary to determine the response of major prey populations to various timber harvest techniques and to rank the quality of owl habitats. Some of these experiments will require landscape scale treatments that are routinely carried out by management. In order to use timber sales as treatments, however, researchers must determine (using a well defined sampling protocol) how treatments are assigned to experimental units (stands or larger land units) and what treatments will be employed.

The link between arboreal lichen and boreal owls depicted in the Envirogram (figure 5, Chapter 9) provides an example of the power of experimentation in developing knowledge necessary to manage boreal owls. The envirogram leads to the hypothesis that red-backed voles (a major winter and summer prey of boreal owls) will be more abundant in forests with greater biomass of *Bryoria sp.* and related lichen. This hypothesis can be tested through a series of laboratory (feeding trial) and field (lichen removal and addition) experiments.

As demonstrated by Korpimäki (1988, 1989), nest boxes can be employed to facilitate experiments with boreal owls. Hayward *et al.* (1993) employed nest boxes in a small experiment examining the relative importance of forest structure vs. cavity availability in nest site selection by boreal owls. Linkages between habitat structure and nesting of boreal owls should be further explored through nest box experiments.

Observational Studies

Many of the gaps in our knowledge cannot be filled through experimental investigation. The historical ecology of forests used by boreal owls will be learned through careful "sleuthing." Hypotheses may be posed and observations (pollen sediment patterns, etc.) used to determine the legitimacy of those hypotheses. Similarly, dispersal patterns of boreal owls will be learned through "simple" observation. Studies of dispersal must discern how dispersing birds react to edges, what habitats they will fly across, etc. Observational studies will also be essential in providing parameter estimates for modeling efforts at many scales and in forming hypothesis to be tested through experimentation. As a consequence of the large home ranges of individual boreal owls, and because of the difficulties encountered in large scale experiments, most field research on boreal owls will involve observational investigations.

Beyond Tools

Examine Boreal Owl Ecology at a Range of Scales

As indicated earlier, a sound conservation strategy will require understanding the response of boreal owls to habitat change on a range of geographic and temporal scales. Research approaches must differ across scales involving different mixes of modeling, experimentation, and observational studies. Studies that examine hypotheses stemming from models built from an expansion of the envirogram presented in Chapter 9 will largely focus on ecological patterns and processes at relatively fine scales (forest stands and small watersheds encompassing one to several square km). At this scale, some experimentation will be possible.

At a broader geographic scale, the response of boreal owls (home range characteristics, population density, productivity, movements) to landscape patterns must be examined. Individual-population dynamics models that examine the sensitivity of various life history characteristics will help focus this research. Gathering the population and behavior

data necessary to answer questions at this scale will require an extensive system of nest boxes facilitating studies in a range of geographic settings. Hayward *et al.* (1992) describe such a system that is similar to the programs established by successful scientists in Europe (e.g., Korpimäki 1981, Sonerud 1985).

Research at the regional scale will largely involve integrating knowledge obtained at finer scales into metapopulation models and then testing the predictions of those models. Empirical information on dispersal of juvenile and adult boreal owls will be critical to developing any metapopulation model. Exercising the metapopulation models to predict future conditions for boreal owls will require sound, spatially specific information from land management plans. Development of sound metapopulation models that examine patterns of boreal owl occurrence over multiple Forest Service Regions will be critical in coordinating management and determining broad research priorities.

Investigate Geographic Variation

Understanding patterns of variation in boreal owl habitat use, demography, population regulation, movement patterns, and food habits will produce many of the insights necessary to manage the species. In European boreal owls, productivity and movements vary geographically. This variation has led to interesting hypotheses concerning the role of various biotic and abiotic factors in boreal owl life history.

Investigate Many Questions on the Same Site

A complex web of interactions is described in the ecological web depicted in figure 5, Chapter 9. Understanding this web will require the integration of studies involving many disciplines — plant ecology, fire ecology, mycology, mammalogy, and community ecology to name just a few. Focusing investigations from many disciplines on common sites will facilitate understanding of the links in this web. These studies should be developed using techniques and approaches employed in population and community ecology.

For example, population and community level investigations of small mammals should be conducted on the same sites as studies of owls. An understanding of small mammal population dynamics and habitat selection will require information on forest structure and dynamics including understory vegetation, fungi, and lichen. The necessary coordination among disciplines is obvious.

Coordinating interdisciplinary research is not trivial, however. Much has been written about the value of interdisciplinary studies but far less published resulting from such work. Initiating coordinated investigations to understand boreal owl ecology may not be easy. By initiating some studies at existing, long-term ecological research sites, some of the logistic problems could be solved.

Small-Scale Demography

Although ignored for a while in applied wildlife research, demographic studies are becoming a cornerstone upon which conservation programs are built (Dennis *et al.* 1991, Verner *et al.* 1992). Examination of population trend and analysis of the sensitivity of λ to variation in survival and reproduction have been the focus of some investigations. In some efforts, estimation of λ for whole populations was sought.

A potentially more efficient approach would estimate demographic characteristics for small groups of individuals and look for patterns relating demography to characteristics of the environment. These investigations could be approached in an observational or experimental framework. In either case, a system of nest boxes as described in Hayward *et al.* (1992) will facilitate obtaining some of the required data. Without nest boxes it will be extremely difficult to obtain a sample of owls sufficient to answer most questions. Of course, nest boxes cannot be used to answer some questions concerning nesting habitat and must be employed judiciously to avoid biasing results. Studies in Europe by Korpimäki (1981), Sonnerud (1985), Lofgren *et al.* (1986) and others have demonstrated the power of nest boxes in studying this species.

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Part IV: GREAT GRAY OWLS

Current Management Situation: Great Gray Owls

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The breeding range of great gray owls (*Strix nebulosa*) in the United States includes portions of Alaska, mountains in the western United States including portions of the Cascades and Sierra Nevada ranges and the northern Rockies, and portions of Minnesota, Michigan, Wisconsin, and New York (see Chapter 14 and Map 3). The species is sometimes observed in more southerly states during severe winters. Based on the species' documented distribution (see National Geographic Society 1987, Johnsgard 1988, and others), the owl may occur on National Forests across seven Regions. To document the management status of great gray owls throughout its range we queried management personnel on all National Forests where the species is likely to occur. Our questionnaire requested information on:

1. Documented breeding status of great gray owls on the National Forest (no records, recorded, recorded breeding).
2. The range of habitats in which the species has been recorded on the Forest.
3. The existence of any Forest or Regional level conservation strategies and/or management plans.
4. The management status of the species in each Region (state list, USDA Forest Service's sensitive species list).

5. Whether forests are conducting distribution surveys for great gray owls.

6. The distribution of great gray owls plotted on a National Forest, map based on all data available from the Forest data base.

The questionnaire asked for additional, more qualitative, information. For instance, we asked how Forests are dealing with this species in biological evaluations (evaluating important habitat or population viability) and in monitoring plans. We were also interested in whether Forests had information on changes in vegetation used by great gray owls over the last 2 centuries.

We also reviewed refereed literature sources for documented owl sightings and locations where museum specimens were collected. Most of these locations were plotted using U.S. Geological Survey 7.5" topographic maps. Where definite locations could be obtained they were plotted based on the latitude and longitude of the site. When locations were not clearly defined or described, the approximate center of the appropriate U.S. Geological Survey 7.5" topographic map was used. In some cases only the county of occurrence was retrievable from the literature. In these cases, the location is shown as a county center.

Table 1.—Status of great gray owl on National Forests as reported by managers early in 1993.

Region	No. of Forests in Region	No. of Forests where owl is present	No. of strategies or plans in place	Addressed in Forest management plan?	Forest Service conservation status
Northern	13	12	None	No	None
Rocky Mountain	12	2	None	No	None
Southwestern	11	Does not occur in this Region			
Intermountain	16	8	None	No	Sensitive
Pacific Southwest	18	10	None	No	Sensitive
Pacific Northwest	19	14	None	7 forests	None
Eastern	14	1	1	1 forest	None
Alaska	4	4	None	No	None

Table 2.—Habitat associations of great gray owls based on surveys of USDA Forest Service data bases. Habitat is described by dominant overstory tree species: SF - Spruce-fir forest, LP - Lodgepole pine forest, DF - Douglas fir forest, MC - Mixed conifer forest, WBP - White-bark pine forest, PP - Ponderosa pine forest, GF - Grand fir forest, QA - Quaking aspen forest, LBP - Limber pine forest, RF - Red fir forest. Status for National Forests who did not respond is listed as "not present."

State	Forest	Occurrence	Habitats
Northern Region (Region 1)			
Montana	Beaverhead	Present	SF, LP
Montana	Bitterroot	Present	
Idaho	Idaho Panhandle	Present	
Idaho	Clearwater	Present	DF, LP
Montana	Custer	Suspected	LP, DF ~7000 ft.
Montana	Deerlodge	Present	LP, DF
Montana	Flathead	Present	
Montana	Gallatin	Present	
Montana	Helena	Suspected	
Montana	Kootenai	Present	
Montana	Lewis and Clark	Present	High elevation MC, WBP, LP, SF
Montana	Lolo	Breeding	~7200 ft., LP, SF
Idaho	Nez Perce	Suspected	
Rocky Mountain Region (Region 2)			
Wyoming	Bighorn	Present	
South Dakota	Black Hills	Not present	
Colorado	Grand Mesa	Not present	
Wyoming	Medicine Bow	Not present	
Colorado	Rio Grande	Not present	
Colorado	Arapaho/Roosevelt	Not present	
Colorado	Routt	Not present	
Colorado	Pike/San Isabel	Not present	
Colorado	San Juan	Not present	
Wyoming	Shoshone	Present	
Colorado	White River	Not present	
Nebraska	Nebraska	Not present	
Intermountain Region (Region 4)			
Utah	Ashley	Suspected	LP/SF
Idaho	Boise	Suspected	
Wyoming	Bridger-Teton	Breeding	MC
Idaho	Caribou	Breeding	Mature DF/LP
Idaho	Challis	Breeding	LP
Utah	Dixie	Not present	
Utah	Fishlake	Not present	
Nevada	Humboldt	Not present	
Utah	Manti-La-Sal	Not present	
Idaho	Payette	Breeding	DF, PP, GF/QA
Idaho	Salmon	Breeding	SF, LBP
Idaho	Sawtooth	Not present	
Idaho	Targhee	Breeding	LP, DF, MC
Nevada	Toiyabe	Breeding	LP, MC
Utah	Uinta	Not present	
Utah	Wasatch-Cache	Not present	
Pacific Southwest Region (Region 5)			
California	Angeles	Not present	
California	Cleveland	Not present	
California	Eldorado	Not present	
California	Inyo	Suspected	

Table 2. - (Continued),

California	Klamath	Suspected	
California	Lassen	Present	MC
California	Los Padres	Not present	
California	Mendicino	Not present	
California	Modoc	Present	SF
California	Six Rivers	Not present	
California	Plumas	Present	RF, MC
California	San Bernardino	Not present	
California	Sequoia	Present	RF, MC, PP
California	Shasta-Trinity	Suspected	
California	Sierra	Suspected	
California	Stanislaus	Present	SF
California	Tahoe	Present	RF, MC, LP
California	Lake Tahoe	Not present	

**Pacific Northwest Region
(Region 6)**

Oregon	Deschutes	Breeding	LP, MC,
Oregon	Fremont	No response	
Washington	Gifford Pinchot	Present	
Oregon	Malheur	Present	
Washington	Mt. Baker	Present	
Oregon	Mt. Hood	Not present	
Oregon	Ochoco	Not present	
Washington	Okanogan	Breeding	
Washington	Olympic	Present	
Oregon	Rogue River	Breeding	LP
Oregon	Siskiyou	Present	
Oregon	Siuslaw	Not present	
Oregon	Umatilla	Breeding	
Oregon	Umpqua	Present	MC
Oregon	Wallowa-Whitman	Breeding	MC
Washington	Wenatchee	Present	MC
Oregon	Willamette	Breeding	
Oregon	Winema	Present	
Washington	Colville	Not present	

**Eastern Region
(Region 9)**

Wisconsin	Chequamegon	Not present	
Minnesota	Chippewa	Not present	
Michigan	Huron-Manistee	Not present	
Missouri	Mark Twain	Not present	
Wisconsin	Nicolet	Not present	
Michigan	Ottawa	Not present	
Illinois	Shawnee	Not present	
Minnesota	Superior	Breeding	?
Michigan	Hiawatha	Not present	
Pennsylvania	Allegheny	Not present	
Vermont	Green Mt.-Finger Lake	Not present	
West Virginia	Monongahela	Not present	
New Hampshire	White Mountain	Not present	
Indiana	Wayne-Hoosier	Not present	

**Alaska Region
(Region 10)**

Alaska	Tongass-Stikine	Present	
Alaska	Tongass-Chatham	Present	
Alaska	Chugach	Present	
Alaska	Tongass-Ketchikan	Present	

The distribution of great gray owls based on literature and agency locations is depicted in Map 3. The distribution of major vegetation associated with great gray owls was not plotted because of the wide range of forest types used by this species throughout its range. The owl locations were digitized and plotted on an existing map of the United States.

Great gray owls were reported to occur on 51 of 96 Forests in seven Regions. The owl has been recorded breeding on 15 of these forests. The great gray owl is listed as a USDA Forest Service "sensitive species" in two regions and on the Superior National Forest in a Region where the owl has no special status (table 1). In addition to its designation as a sensitive species by the Forest Service, great gray owls are given special management status in three states: Idaho (Species of Concern), Montana (Species of Concern), and California (endangered). The Committee on the Status of Endangered Wildlife in Canada considers great gray owls "vulnerable" or "a species at risk because of low or declining numbers" (Nero 1980). Specific Forest-level management recommendations have been written for nine National Forests. None of these can be considered management plans or strategies. Management guidelines on most forests involve very general direction to protect nest sites or to protect raptor nests in general. On the Payette National Forest, recommendations include general direction to manage foraging as well as nesting habitat and to manage prey populations.

Although many forests report the presence of great gray owls, there is little information on population or habitat trends. Surveys to establish the distribution of great gray owls are being conducted in the Intermountain and Alaska Regions while the owls are being located during surveys for spotted owls (*Strix occidentalis*) in the Pacific Southwest (where the species is listed as sensitive) and Pacific Northwest Regions (table 2). Surveys directed at the spotted owl could lead to a biased view of the distribution of great gray owls because of the different habitats used by the two *Strix* owls.

The response we received from National Forests throughout the range of great gray owls indicates that little is known about the species in these management units. Furthermore, there is no mechanism in place to gather the data necessary for management. The Forests where some attempt has been made to manage great gray owls have concentrated management on nesting habitat, focusing on the short-term objective of protecting currently occupied nests.

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Review of Technical Knowledge: Great Gray Owls

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INTRODUCTION

The great gray owl (*Strix nebulosa*) is the longest, but not heaviest, of the northern forest owls. Distributed holarctically across the boreal forests of North America and Eurasia, the great gray owl extends its range southward into the contiguous states by inhabiting forests other than the boreal type. The subalpine and montane forests of the Cascade Range, Sierra Nevada Range, and the Rocky Mountains support great gray owl populations in central Washington; central and northwestern Oregon; north-central and eastern California; northern, central, and southeastern Idaho; western Montana; and northwestern Wyoming. Despite its large size, broad distribution, and relatively bold nature, the great gray owl remains poorly understood. European investigations focus primarily on how *Microtus* populations affect the owl's productivity and movements (Hilden and Helo 1981, Mikkola 1983, Stefansson 1983, Cramp 1985, Korpimäki 1986). We have found no studies that examine great gray owl population characteristics or habitat use. In North America, Bull *et al.* (1988a, 1988b, 1989a, 1989b) intensively studied great gray owl demography, movements, and habitat use. Their study area in northwestern Oregon, however, may not be characteristic of the entire North American range. Franklin (1988) observed the breeding biology of great gray owls in southeastern Idaho. Duncan (1992) examined great gray owl movements as they relate to several factors, including prey abundance, for a Canadian population. The remaining studies (e.g., Winter 1986, Osborne 1987, Spreyer 1987) are largely limited to describing nest sites. Though the great gray owl has not been targeted for expansive ecological studies, a useful body of knowledge has accumulated through more specific research and incidental sources.

DISTINGUISHING CHARACTERISTICS

Distinctly colored, the great gray owl wears a dusky gray to sooty overall plumage. Grayish white

mottles the crown, nape, back, rump, and shoulders; but the underparts are boldly streaked over fine barring. Its wings and long, wedge-shaped tail are strongly barred. The great gray owl's head supports no horn-like feather tufts, but the facial disk, common to all owls, is conspicuously patterned with concentric bands of pale gray on a dusky white background. Bright yellow eyes punctuate the face and appear small for the size of the bird. The yellow or ivory bill contrasts a black chin sharply defined by prominent white jowl patches. The legs, feet, and toes are completely feathered. Great gray owls exhibit pronounced reversed size dimorphism (McGillivray 1987). Males weigh 700-1,175 g and females 925-1,700 g (Duncan 1992). Total length is 61-84 cm. Cramp (1985) and Voous (1988) provide measurements from the Palaearctic.

SYSTEMATICS

The great gray owl is the only member of the genus *Strix* that breeds in both the Old and New Worlds (Voous 1988). Of the two recognized subspecies, *Strix nebulosa nebulosa* inhabits North America and *Strix nebulosa lapponica* inhabits Europe and Asia. Although minor plumage differences exist between the subspecies, Oeming (1955), Mikkola (1981), and Duncan (1992) concluded that the two subspecies were very similar in size. The size similarity probably reflects three important circumstances. First, diet, climate, and other ecological factors are similar across the species' range. Second, the species is probably a recent arrival to North America (Oeming 1955, Voous 1988). Third, current theory (Eldredge and Gould 1972) suggests the great gray owl exhibits species stability. Sibley and Ahlquist (1990) used DNA analysis to identify the mottled owl (*Ciccaba virgata*) and the barred owl (*Strix varia*) as the great gray owl's closest relatives.

Strix nebulosa is not represented in the fossil record of North America. However, fossil material does yield related species (Olson 1985). *Strix dakota* (Miller 1944:95) has been found in South Dakota's Tertiary

deposits. Dating back 18-19 million years, *S. dakota* was associated with the early Hemingfordian group in the North American Land Mammal Age (NALMA). Unlike living species in this genus, it was a small owl, and Ford (1967:69) has questioned its generic allocation. A fossil tarsometatarsus of an undescribed *Strix* species dates back 9 million years to the late Clarendonian-early Hemphillian (NALMA) group in the Tertiary deposits of north-central Nebraska. It is in the size range for males of *Strix nebulosa*. Finally, Olson has commented on two late-Pleistocene specimens (Olson 1984:44-46). One of them, an unnamed species of *Strix* from Ladds, Georgia, was larger than any living North American owl. *Strix brea* from Rancho La Brea, CA (Howard 1933:66), was comparable to *Strix nebulosa* in size except that it had very long tarsometatarsi.

DISTRIBUTION AND ABUNDANCE

North American Breeding Range

In Canada, the great gray owl ranges from near tree line in northern Yukon, northwestern and central Mackenzie (Lockhart River, Great Slave Lake), northern Saskatchewan, northern Manitoba (Churchill, The Pas), and northern Ontario (probably Severn River, Moose Factory) south through southern Yukon and interior British Columbia, northern and central Alberta, central Manitoba (Dauphin Lake, South Junction), and central Ontario (Godfrey 1986); it also occurs in Quebec but breeding has not been confirmed in this province. In the United States, great gray owls nest commonly in central and southern Alaska; but the species exhibits uneven distribution throughout its southern range, which includes central and northwestern Washington, northern and central Idaho, western Montana, northwestern Wyoming, northeastern and central Oregon, east-central California, west-central Nevada, and portions of Minnesota, Michigan and Wisconsin (Map 3).

North American Winter Range

The winter range of the great gray owl coincides with its breeding range except for a tendency to wander irregularly south in winter (Nero 1969, Brunton and Pittaway 1971), occasionally as far as Pennsylvania and Long Island, New York, in the east. Movement patterns of southwestern populations are unknown but are thought to be more stable and sedentary (Duncan 1992, Bull and Duncan 1993).

Eurasian Range

In Eurasia, great gray owls breed from northern Scandinavia, northern Russia and northern Siberia south to central Russia, northern Mongolia, northern Manchuria, Amurland, and Sakhalin (Cramp 1985). Southern extensions in boreal forest of some central Asiatic mountains (Salair and Kuznetsk Alatau in the northern Altai and the Kentei Mountains in eastern Mongolia at 54°N) correspond to similar extensions into the Rocky and Sierra Nevada Mountains in the United States (Voous 1988).

Abundance

Counts or estimates of great gray owl abundance differ among studies and are likely influenced by estimate methods, researcher bias, the phase of prey cycle in northern populations, and nest site availability. Nero (1969) estimated the North American great gray owl population to be between 5,000 and 50,000 birds. This estimate was arbitrary and not based on a sample from the "population" of interest. The highest reported nesting density in North America is 1.88 pairs/km² in Manitoba and northern Minnesota (Duncan 1987). Bull and Henjum (1990) calculated densities of 1.72 pairs/km² and 0.74 pairs/km² on two Oregon study sites. Their calculations were based on nests located during systematic searches. Winter (1986) recorded a nesting density of 0.66 pairs/km² in California. Spreyer (1987) recorded 0.15 pairs/km² in Minnesota. These study areas were generally chosen because great gray owls were abundant in the area.

European researchers report substantially higher maximum densities. In fact, some classify the species as a "loose colonial nester" that is extremely tolerant of intraspecifics on its breeding home range (Wahlstedt 1974, Mikkola 1983, Duncan 1987, Bull and Henjum 1990). Wahlstedt (1974) discovered 7 pairs over a distance of 3 km in Sweden. Hoglund and Lansgren (1968) documented nests in Sweden as close as 100 m apart. In Finland, 3 nests were found within 400 m of one another (Mikkola 1976). Although nests may be clumped, the species' breeding strategy does not fit the definition of a colonial nester (Lincoln *et al.* 1982).

Population Trends

No long-term, rigorous, or standardized data on regional or local breeding populations are available. At a local scale, southern populations in the west-

ern United States are thought to be relatively stable with individuals breeding every year and/or at least remaining in the same general area all year (Winter 1986, Bull and Henjum 1990). Northern populations appear to be less stable (Nero 1980, Duncan 1992). Duncan (1992) related great gray owl population stability to that of prey biomass productivity (see the Food Habits section later in this chapter).

The North American Breeding Bird Survey (BBS) methodology does not effectively detect nocturnal species. A standardized survey protocol specific to great gray owls, or to owls in general, needs to be used across the species' range if long-term population trend data are to be obtained. Local population studies from within the breeding range for North America (Collins 1980, Nero 1980, Winter 1986, Franklin 1987, Bull and Henjum 1990, Duncan 1992) and Eurasia (reviewed in Mikkola 1983) typically last fewer than 8 years. Caution must be exercised in drawing regional, or even local, population trend conclusions from short-term studies where prey populations are cyclic or fluctuate multi-annually (see also Movements).

Breeding populations of Finland's great gray owls showed long-term regional increases from 1954 to 1981, but these probably related to more intensive search efforts and to an increasingly colder climate (Mikkola 1983). Collins and Wendt (1989) summarized breeding bird survey data for many Canadian birds from 1966 to 1983. For species with low densities, they compared a simple abundance index for the time periods 1966-1977 and 1978-1983. Great gray owls were detected in 4 of 10 Canadian regions covered by the BBS. Between the two periods, increases were noted in the maritime provinces, central Ontario and Quebec, and southern British Columbia whereas a decrease was noted for the central prairies. Collins and Wendt (1989) caution against inferring regional population trends for species with such low densities or small samples and they say that changes noted are possibly due to changes in BBS techniques. Fyfe (1976) reviewed the population status of raptors in Canada based on correspondence with bird observers. Great gray owl population trends were noted as "fluctuating" in Ontario, southern Quebec, the prairie provinces, and British Columbia. Trends were reported as "unknown" for the Northwest Territories and the maritime provinces. Nero *et al.* (1984) speculated that more great gray owls now inhabit southern Manitoba than in the past.

Conversely, Winter (1986) surmised from limited data that great gray owl populations in California have declined from ancestral levels due to habitat

degradation. A breeding population in the Targhee National Forest, Idaho, increased then decreased from 1974 to 1989. Groves and Zehntner (1990) felt the changes were related to a specific timber harvest regime but this speculation was also based on limited data rather than on long-term monitoring. Bryan and Forsman (1987) believed Oregon populations must have declined as a result of habitat loss since all ($n = 63$) of their locations occurred in mature to old-growth timber, but the suspected decline cannot be substantiated.

No data substantiate historical changes in distribution although some have suggested possible changes in Europe (Mikkola 1983, Voous 1988) and in North America (Oeming 1955, Nero 1980). Reliable information on population trend and changes in great gray owl distribution will only become available after monitoring programs have been in place for several years.

MOVEMENTS

Great gray owls have been described as both nonmigratory and nomadic (Nero 1980, Mikkola 1983). Movement patterns are variable, being stable in some areas and/or years while highly irruptive in others. Movements appear to be influenced by prey availability and the stability of prey biomass productivity (Nero 1980, Mikkola 1983, Duncan 1992). In southern latitudes great gray owls appear to shift to lower elevations and, presumably, lower snow depths (J. Winter; pers. comm., Franklin 1987). In northeast Oregon adult owls moved 2-43 km from their nest sites to areas with thinner snow cover (Bull *et al.* 1988a); but 39% of radio-marked pairs nested on the same nest site a second year, and 39% nested within 1 km of their previous nests. Only 22% nested > 1 km from their previous nests and the average distance between successive nests was 1.3 km (0.2-4.5 km).

In boreal forests of Canada and Alaska, individuals can migrate up to 700 km (Nero 1980, Duncan 1992). In Manitoba and northern Minnesota, migration (breeding dispersal, c.f. Greenwood and Harvey 1982) is generally independent of snow cover. Among dispersing birds 62% of females and 27% of males moved before snow accumulated, and all adults dispersed before snow depths reached 45 cm. In fact, although great gray owls dispersed to areas of lower elevation, snow levels increased. Dispersal did, however, follow rodent population crashes (Duncan 1992); and interaction between dispersal strategy and prey population phases was significant ($P < 0.001$). Owls failing to disperse following prey

declines frequently die (Duncan 1992). Cramp (1985), however, noted no correlation in European literature between the *extent* of movement and rodent population levels.

For North America, records of irregular southward winter invasions of this species date back to 1831 when at least one individual flew as far south as Marblehead, Maine. Other winter incursions are reported by Godfrey (1967), Collins (1980), Nero (1980), and Campbell *et al.* (1990). See also figure 1. Large invasions rarely occur in all or many regions in the same year, implying asynchronous prey population crashes over large regions (Duncan 1992). Nine sporadic great gray owl invasions between 1955 and 1981 have been observed (generally in different years from North America) in Scandinavia (Cramp 1985). This species is known to occasionally winter well north (as well as south) of its taiga breeding range (Dement'ev and Gladkov in Nero 1980, Cramp 1985).

Duncan (1992) also documented that breeding great gray owls in southeastern Manitoba and northern Minnesota (within the southern portion of their North American taiga breeding range) disperse northward following prey population crashes. This

dispersal more closely resembles a migratory type dispersal rather than nomadism (c.f. Baker 1978). Radio-tracking shows individuals can travel (day and night) up to 40 km in 24 hours and 650 km in 3 months (Duncan 1992). Great gray owls loosely congregate, probably in response to abundant prey (Nero 1980, Duncan 1992). For example, during the winter of 1978-1979, about 40 birds gathered near Toronto, Ontario; and >100 were found in southeastern Manitoba within a 30 km radius (Bull and Duncan 1993).

Sex Differences

In Manitoba and northern Minnesota, radio-marked adult females migrated farther and earlier (mean = 372 km; October) than did adult males (235 km; January-February) but no gender difference was observed in mean direction of migration (Duncan 1992). Sex ratios were calculated by Duncan (1992) based on winter-caught great gray owls ($n = 412$) sexed by discriminate function analysis. For a combined 14-year period, sex ratios were significantly female biased (294 females:118 males).

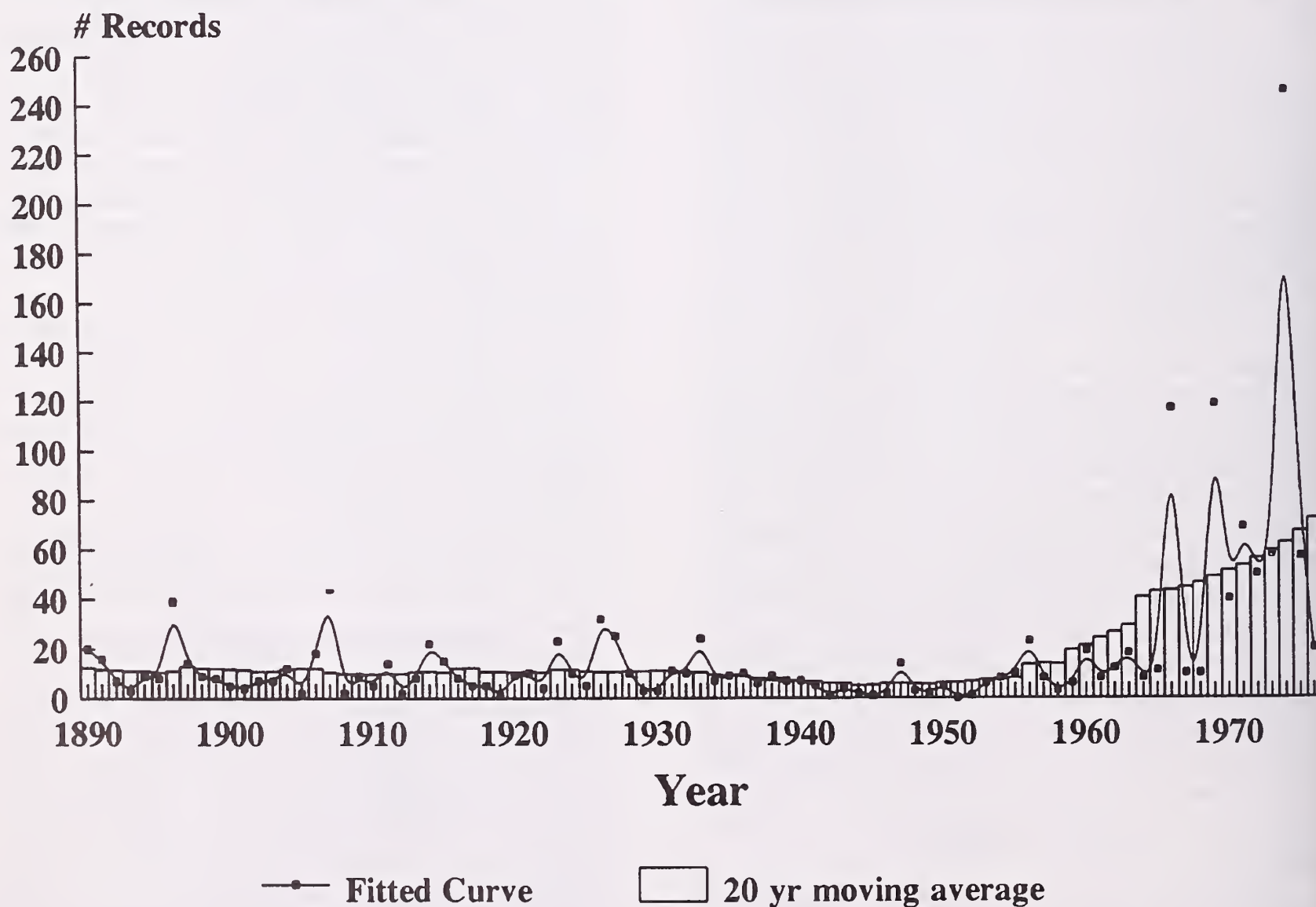


Figure 1.--Numbers of great gray owls observed in southern Canada and northern United States during winter 1890-1979 (data from Collins 1980).

HABITAT USE

Few experimental studies have analyzed habitat associations, although Servos 1986, Bull *et al.* 1988b, and Bouchart 1991 conducted qualitative studies. Abundant anecdotal descriptions of owl-occupied habitat exists. Availability of nest sites and suitable foraging habitat are considered the most important factors governing habitat use by breeding great gray owls (Lundberg 1979, Collins 1980, Nero 1980 Mikkola 1983).

Nesting Habitat

Nest Structure

Great gray owls rely on old hawk and raven stick-nests or natural depressions on broken-topped snags or stumps for nest sites (Nero 1980, Mikkola 1983) (see tables 1 and 2). They also nest on natural platforms formed by dwarf-mistletoe (*Arceuthobium spp.*) and, rarely, on the ground, rock cliffs, or haystacks (Mikkola 1983, Duncan 1992). Great gray owls readily accept artificial nest structures (Nero *et al.* 1974, Collins 1980, Bohm 1985, Bull and Henjum

1990). Thus, the actual nest structure and its support may be relatively unimportant in nest site selection compared to the nest site habitat and availability of foraging habitat. In evaluating long-term habitat quality, it is important to consider factors that influence populations of nest-building species (*Accipitridae* and *Corvidae*) and tree-pathogen/insect interactions that can influence tree branching. Some authors report that the relative use of broken-topped snags decreases northward through the great gray owl's breeding range (Mikkola 1983, Winter 1986, Franklin 1987) corresponding with a decrease in tree size and circumference in northern latitudes.

Broad Scale Nesting Habitat

In Canada great gray owl breeding habitat is generally described as extensive taiga interspersed with sphagnum bogs, muskegs, and other open spaces (Nero 1980, Harris 1984, Godfrey 1986, Campbell *et al.* 1990, Semenchuk 1992). Tamarack (*Larix laricina*) bogs appear to be preferred nesting habitat in Manitoba (Nero 1980, Servos 1986, Lang *et al.* 1991, Duncan 1992). In southeast Manitoba three studies have investigated breeding habitat used by great gray owls, primarily at the forest stand scale. Ser-

Table 1. – Tree species used for nesting (1), or dominant trees in nest stands (2) used by great gray owls in Canada and the United States. A "3" designates tree species used for nesting that also represent the dominant tree in nest stands. Data from: Bouchart (1991), Osborne (1987), Spreyer (1987), Harris (1984), Nero (1980), Duncan (1992), Servos (1986), Bull & Henjum (1990), Winter (1986), Oeming (1955), Campbell *et al.* (1990), Semenchuk (1992), Kondla (1973), and Sent (1938). Tree species abbreviations: LL *Larix laricina*, PT *Populus tremuloides*, PB *Populus balsamifera*, PS *Populus spp.*, PI *Picea inariana*, PG *Picea glauca*, BP *Betula papyrifera*, TO *Thuja occidentalis*, AB *Abies balsamea*, PB *Pinus banksiana*, FN *Fraxinus nigra*, TA *Tilia americana*, UA *Ulmus amaricana*, AS *Acer saccharum*, AR *Acer rubrum*, PC *Pinus contorta*, PP *Pinus ponderosa*, PM *Pseudotsuga menziesii*, PE *Picea engelmannii*, LD *Libocedrus decurrens*, AC *Abies concolor*, LO *Larix occidentalis*.

Location	Tree species																			
	LL	PT	PB	PS	PM	PG	BP	TO	AB	PB	FN	TA	UA	AS	AR	PC	PP	PM	PE	LD
Ontario	3	3	1		3					1										
Manitoba	3	3	1	1	2		2	1	1				1							
Saskatchewan	3	3			2															
Minnesota	3	2	3				1				1	1	1		1					
Wisconsin	3	3																		
Alberta	1	3	3	1	1	2				1										
British Columbia		3			3	1										2		2	2	
Alaska			3			3	2													
Northwest Territories						3														
Yukon																				
Washington																2	2	2		2
Idaho		3		1												3		3	1	
Montana																				
Oregon																3	3	3		3
Wyoming		3		1												3		3	1	
California																	2			2

Table 2.—Nest platform types used by great gray owls in Canada and the United States. See table 1 for sources.

Location	Stick	Stump	Witch's broom	Ground	Artificial
Ontario	x	x			
Manitoba	x	x		x	x
Saskatchewan	x				
Minnesota	x				x
Wisconsin	x				
Alberta	x				x
British Columbia	x		x		
Alaska	x	x			
Northwest Territories	x				
Yukon	x				
Washington	x	x			
Idaho	x	x			x
Montana	x	x			
Oregon	x	x	x		x
Wyoming	x	x			x
California		x			x

vos (1986) looked at habitat use by post-fledging family groups rather than actual nest sites. The dominant tree species within a 1-km radius around 14 nest sites were tamarack (6), quaking aspen (*Populus tremuloides*) (4), black spruce (*Picea mariana*) (2), paper birch (*Betula papyrifera*) (1), and tree-grown muskeg (1). The distribution of these sites reflected the availability of habitat (Bouchart 1991). Collins (1980) looked at dominant tree species in nest stands within 800 m of 9 nests in southeastern Manitoba. Tamarack/black spruce dominated at seven sites and quaking aspen dominated at the others. See table 1 for descriptions of other sites.

Tamarack and black spruce wetlands were associated with 25 of 27 suspected breeding sites in Saskatchewan (Harris 1984). In Alberta, Oeming (1955) found that great gray owls frequently nested in poplar woods adjacent to extensive treed muskegs. Spreyer (1987) conducted a detailed floristic analysis within 20 m of 14 nest sites in Minnesota. Nest site stands were dominated by hardwood tree species, especially black ash (*Fraxinus nigra*), basswood (*Tilia americana*), American elm (*Ulmus americana*), red maple (*Acer rubrum*), and sugar maple (*Acer saccharum*). All were characterized as being in habitats with high soil moisture.

Great gray owls bred in forests (all types) in the vicinity of marshes, lakes, muskegs, wet meadows, and pastures in British Columbia (Campbell *et al.* 1990). The forests were primarily Douglas-fir (*Pseudotsuga menziesii*) with patches of aspen but also Douglas-fir/lodgepole pine (*Pinus contorta*), lodgepole pine/Engelmann spruce (*Picea engelmannii*),

black spruce, and Engelmann spruce-dominated stands between 900 and 1,220 m elevation. In Alaska, great gray owls nested primarily in balsam poplar (*Populus balsamea*) forest and less frequently in white spruce/birch forest (Osborne 1987).

In southern parts of their range, great gray owls nest in relatively xeric, montane evergreen, or deciduous forests up to 2,800 m elevation. Winter (1986) and Reid (1989) concluded that access to suitable hunting meadows restricts population densities and range expansion in California since owls rarely foraged in forest habitat. For example, preferred breeding habitats were pine and fir forests adjacent to montane meadows between 750 m and 2,250 m elevation (Winter 1986). Ponderosa pine (*Pinus ponderosa*) was the dominant tree species within the home ranges of breeding owls, followed by incense cedar (*Calocedrus decurrens*) and white fir (*Abies concolor*). In southeastern Idaho and northwestern Wyoming, 10 nests were in mid- to late-successional stages of Douglas-fir forests on flat land with herbaceous understory, which is the most abundant habitat available (Franklin 1987). In addition, clear-cut and natural meadows were associated with all 10 nests. More than 90% of sightings of this species in Idaho and Wyoming were in the lodgepole pine/Douglas-fir/aspen zone (Franklin 1987). In central Oregon, meadow systems associated with coniferous forests were used (Bryan and Forsman 1987). In northeastern Oregon, all forest types sampled had nests, with 50% found in Douglas-fir/grand fir (*Abies grandis*) forest types, 29% in lodgepole pine/western larch, 15% in ponderosa pine/Douglas-fir, and 7% in pon-

derosa pine (Bull and Henjum 1990).

Mikkola (1983) found that great gray owls in Finland use damp heath coniferous forests (45%), spruce bogs (35%), dry heath coniferous forests (11%), pine peat bog (6%), and other herb-rich forests (3%). These were also associated with open grassy areas.

Home Range Area

Great gray owl home ranges are often relatively small, depending on food supply (Mikkola 1981). Average home range size calculated for breeding adults in Oregon was 4.5 km² (n = 5 males, range 1.3 - 6.5 km², minimum convex polygon [MCP]) (Bull *et al.* 1988a, Bull and Henjum 1990). Craighead and Craighead (1956) calculated 2.6 km² (MCP) in Wyoming. Males have been observed hunting up to 3.2 km from their nest (Bull and Henjum 1990). Maximum distance traveled by adults from their nest averaged 13.4 km (Bull and Henjum 1990). Bryan and Forsman (1987) observed owls moving 3-4.8 km/d.

Microhabitat

Nesting

Bull and Henjum (1990) erected 158 artificial platforms to determine preference for nest type (open vs. box), height (9 m vs. 15 m), and distance to a clearcut (adjacent vs. 100-200 m). Great gray owls always chose open structures, preferred higher nest structures, and selected nest sites within forest stands. Distance to the nearest opening averaged 256 m (range 0 to 1,000 m) in Manitoba (Bouchart 1991) and 143 m in Idaho and Wyoming (Franklin 1987). Canopy closure exceeded 60% at most Oregon nest sites (Bull and Henjum 1990), and the percentage of forested area within 500 m radius of nests varied between 52% and 99%.

Roosting

Great gray owls typically roost in trees near the trunk. They lower their heads, close their eyes, and "fold" their facial disks, thus dividing the face with a vertical dark line that often matches the bark pattern (Cramp 1985). They roost in trees with fairly dense canopy during hot weather and close to the trunk in inclement weather. Winter (1986) noted that great gray owls roosted at lower heights during warmer weather, possibly as a thermoregulatory response. In California, roosts averaged 90 m from openings and 10.9 m above ground; trees <23 cm dbh were avoided (Winter 1986).

Unlike spotted owls, which roost in the same location over long periods (Forsman 1976, Winter 1986), great gray owls frequently change trees to roost throughout their home range. In winter and late spring (April), owls occasionally roost in sunny open areas and atop snags (Winter 1986, Bull and Duncan 1993). Although great gray owls frequently use meadows for foraging, they typically roost away from the meadow's edge. Winter's (1986) roosts averaged 90 m from openings and Bryan (1985) also noted owls roosting within forest stands.

Because fledglings leave the nest before they can fly, forested habitat around the nest is considered important for their survival. Bull and Henjum (1990) noted that roosts accessible to flightless young, such as leaning and deformed trees and perches high enough to avoid terrestrial predators, may increase reproductive success. In another study area, roost height correlated positively with the age of recently fledged young (Franklin 1987).

Foraging

Several authors cite foraging habitat throughout the great gray owls' range as relatively open, grassy habitat, including bogs, selective and clear-cut logged areas, natural meadows, and open forests (Nero 1980, Mikkola 1983, Winter 1986). These authors maintain that great gray owls avoid hunting in timbered stands. Bryan and Forsman (1987) and Bull and Henjum (1990), however, report great gray owls foraging in and, in fact, preferring open forests for foraging. In northeast Oregon, male owls foraged in stands with 11-59% canopy closure (Bull and Henjum 1990). These stands had heavy ground cover (average 88%) dominated by grasses. While hunting, great gray owls perch at varying heights but usually 3-5 m high in both live trees and snags adjacent to or within open grassy areas. Perch heights for Oregon males averaged 5.5 m (Bull and Henjum 1990). Great gray owls rarely hunt while sitting on the ground or while flying (Collins 1980, Nero 1980, Winter 1986, Duncan 1987, Reid 1989, Bull and Henjum 1990). Perch to prey distances averaged 10.5 m in Bull and Henjum's (1990) study. Downed wood was present within 1 m of the capture point at 77% of prey capture sites (Bull *et al.* 1988b).

Based on relocations of radio-marked individuals (five males, five females and six young), Servos (1986) found that owls in southeastern Manitoba used tamarack bogs and treed muskeg in greater proportion than their availability. Jack pine (*Pinus banksiana*), black spruce stands, open areas with few or no trees, and habitats with dense shrub layers were avoided (Servos 1986).

Winter Use

Winter habitat is generally the same as the breeding habitat. In some mountainous portions of its breeding range, the great gray owl often descends to lower elevations (Yosemite National Park, California: J. Winter, pers. comm.). The ecotone between grassland meadows and tall willows, balsam poplars and white spruce (*Picea alba*), is the preferred winter habitat in Alaska (Osborne 1987). In Manitoba, the owls use tamarack, black spruce, and aspen forests in winter months (Bouchart 1991). Elsewhere in Canada the owl also occupies open fields with scattered large trees, shrubbery, and fence-rows (Brunton and Pittaway 1971, Nero 1969), especially during irruptive winters when many individuals move south.

FOOD HABITS

Great gray owls prey upon relatively small prey. Their diets consist primarily of small mammals, especially rodents. Voles (*Microtus* spp.) dominate their diets over most of their range (Collins 1980, Nero 1980, Mikkola 1983, Bull *et al.* 1989a, Duncan 1992). Pocket gophers (*Thomomys* spp.) are the primary prey in Yosemite National Park, California (Winter 1986), southeast Idaho and northwest Wyoming (Franklin 1988), and northeast Oregon (Bull and Henjum 1990). Occasional prey include shrews (*Sorex* spp., *Blarina brevicauda*, *Microsorex hoyi*), moles (*Scapanus* spp.), red-backed voles (*Clethrionomys gapperi*), deer mice (*Peromyscus maniculatus*), red squirrels (*Tamiasciurus* spp.), flying squirrels (*Glaucomys* spp.), jumping mice (*Zapus* spp.), and

grasshopper mice (*Onychomys* spp). In Canada, star-nosed moles (*Condylura cristata*), northern bog lemmings (*Synaptomys borealis*), heather voles (*Phenacomys intermedius*), least chipmunks (*Eutamias minimus*), weasels (*Mustela* spp.), snowshoe hares (*Lepus americanus*), sharp-shinned hawks (*Accipiter striatus*), broad-winged hawks (*Buteo platypterus*), gray jays (*Perisoreus canadensis*), American robins (*Turdus migratorius*), spruce grouse (*Dendrogapus canadensis*), and wood frogs (*Rana sylvatica*) were also consumed (Duncan 1992).

In most years the great gray owl diet overlaps very little with great horned owls (*Bubo virginianus*), long-eared owls (*Asio otus*), and boreal owls (*Aegolius funereus*). Competition for food is more likely to occur during years when prey species are scarce. In northeast Oregon, the long-eared owl diet is most similar to that of the great gray owl, although the latter eats mostly adult pocket gophers while the former takes juveniles (E.L. Bull, pers. comm.). Whether this difference reflects the owls' diets or sample bias is not clear.

Quantitative data on food habits presented herein are derived primarily from pellet analysis. Prey remains in pellets are a reliable indicator of diet, but caution is needed when analyzing pellets collected at nest sites because breeding males have been observed to deliver larger prey items to the nest and to eat smaller prey themselves (Bull and Henjum 1990).

Great gray owl diets from various locations in North America are compared in table 3. Vole species (weights ranging from 30 to 50 g) dominate diets of northern populations, often comprising > 90% of diets (Hoglund and Lansgren 1968, Mikkola and

Table 3.—Food of the great gray owl from selected regions of North America. Figures indicate percentage of prey by numbers; data derived primarily from analysis of pellets.

Prey	Oregon ¹	Idaho ²	California ³	Manitoba ⁴
<i>Microtus</i>	51.6	34.1	30.8	83.5
<i>Thomomys</i>	28.8	57.9	52.6	—
<i>Sorex</i>	2.2	1.4	1.5	1.6
<i>Peromyscus</i>	0.9	1.6	3.8	0.2
<i>Clethrionomys</i>	13.9	0.7	—	3.0
Bird	0.1	2.2	0.4	1.7
Other	2.5	2.1	10.9	10.0
Prey items (n)	4,546	435	662	2,004

¹Bull *et al.* (1989).
²Franklin (1987).
³Winter (1986).
⁴Duncan (1992).

Sulkava 1970, Pulliainen and Loisa 1977, Mikkola 1983, Osborne 1987). *Microtus* and *Synaptomys* species comprise 91.3% (84% is *Microtus pennsylvanicus*) of great gray owl diets in boreal forest regions of North America (Duncan 1992) and are more similar to that of European great gray owls than to that of owls in Oregon, Idaho, or California. Michigan great gray owls consumed 96% (by number) *Microtus pennsylvanicus* (Master 1979). Cramp (1985) noted that diet varies little between individuals or within years. Even changes between years consist largely of alterations in proportions of vole species rather than the overall proportion of voles. In Manitoba and Minnesota, owls select *Microtus* spp. in proportions greater than their availability, while shrews (Soricidae) and *Clethrionomys* spp. were underutilized (Duncan 1992). In Oregon, however, pocket gophers comprise 67% of the diet's biomass and voles 27% (Bull and Henjum 1990). In California, owls shift prey emphasis between microtines and pocket gophers as prey availability changes (Winter 1986).

In general, peak hunting times are thought to coincide with peak activity of prey species (Nero 1980, Mikkola 1983, Winter 1986, Reid 1989). During the breeding season, the male regularly hunts nocturnally and diurnally in addition to his normal crepuscular pattern. Brunton and Pittaway (1971) reported that in winter great gray owls are crepuscular and diurnal hunters, but great gray owls have also been observed to hunt nocturnally in winter (J.R. Duncan, unpubl. data).

Great gray owls hunt primarily from perches, listening and watching the ground intently. When prey is detected, the owl usually flies only a short distance, generally no more than 50 m. Bull and Henjum (1990) recorded an average perch to prey distance of 10.5 m. Great gray owls can detect and capture prey by sound alone, which permits the capture of prey beneath snow (Law 1960, Godfrey 1967, Nero 1969). Individuals typically hover above the snow and then plunge face downward breaking through the snow with clenched feet and then attempting to grasp prey with their feet and talons (Collins 1980, Nero 1980, Duncan 1992). Nero (1980) observed owls breaking through snow crust hard enough to support an 80-kg person. Great gray owls can reach prey as deep as 45 cm below the snow surface (Collins 1980). Duncan (1992) observed successful foraging in snows exceeding 70 cm. In summer the owls break into the earthen burrows of pocket gophers (*Thomomys* spp.) in much the same way (Tryon 1943, Winter 1986). Bull *et al.* (1989b) observed a 33% capture rate in 90 attacks. Snow-plunging owls achieved

a 65% success rate (Duncan 1992).

Asymmetrical ear openings undoubtedly help this owl detect prey by sound alone, as has been shown experimentally in the barn owl (Payne 1971, see also reviews in Voous 1988 and Marti 1992). Voous (1988) describes the external ear openings of the great gray owl. The asymmetry in the size and position of the great gray owl's ear opening is enhanced by skull asymmetry, which Voous (1988) reports "[promotes] precise directional hearing."

The daily food intake was from 60 to 80 g per day for an incubating wild female (Cramp 1985). In winter, wild adults can consume up to 7 *Microtus*-sized prey (45 g each) per day (Duncan 1992). Bull and Henjum (1990) calculated an individual great gray owl's yearly consumption as > 1,400 voles.

INFLUENCE OF PREY SPECIES BIOLOGY ON OWL MOVEMENTS

Microtine voles generally occupy moist grass/sedge openings and open herbaceous forests (Anderson 1987) whereas pocket gophers (*Thomomys* spp.) prefer drier meadows (Chase *et al.* 1982). Microtines undergo dramatic, geographically asynchronous population fluctuations while pocket gopher populations exhibit less annual variation. The contrasting dynamics of primary prey populations likely influence great gray owl population dynamics. Andersson (1980) compared the relative merits of adult avian nomadism to site tenacity based on a model relating Malthusian fitness of an individual to the pattern of food production. The model predicts that nomadism is most likely when food production fluctuates in an unpredictable manner. Conversely, it predicts site tenacity or migration under stable food production or when fluctuations are regular or predictable. The pattern of food production, then, is likely to influence movements of great gray owls. The semi-nomadic movement pattern of northern populations and the relative site tenacity observed in southern populations fit the predictions of this model.

Northern vole populations are thought to fluctuate with a larger amplitude than southern populations. Explanations for this pattern abound, although none seems completely satisfactory. Hypotheses concerning vole cycles include those based on optimal versus suboptimal habitats (Martell and Fuller 1979), geographical (climatic) gradients (Hansson and Henttonen 1989), dispersal sinks and predation (Tamarin 1978, Gliwicz 1980, Hansson and Henttonen 1989), food and cover (Birney *et al.* 1976, Cole and Batzli 1979, Taitt *et al.* 1981), habitat het-

erogeneity and dispersal (Abramsky and Tracy 1979, Gaines *et al.* 1979, Stenseth 1980), and immunological disfunction and opportunistic, pathogenic microparasitism (Mihok *et al.* 1985). More recently, Halle and Lehmann (1987) investigated the phasic relationship among circadian activity pattern, photoperiod responses, and population cycles in voles. They concluded "that vole population cycles are not triggered by overriding (e.g., climatic) conditions, but depend on population properties themselves." No hypothesis, model (Stenseth 1980), or statistical analysis (Mihok 1981, Garsd and Howard 1981, 1982) has provided an all-encompassing explanation of microtine multi-annual population cycles. Given the diversity of population cycle patterns observed, Lidicker (1988) suggested a multivariate, synthetic approach.

BREEDING BIOLOGY

While great gray owls are typically monogamous, polygyny is occasionally suspected (Cramp 1985, J.R. Duncan, unpubl. data). In boreal forest regions the pair bond does not appear to be maintained over winter. However, individuals may nest with the same mate in the subsequent year if local prey populations remain high (Duncan 1992). In Oregon, Idaho, and California, pairs possibly remain together as long as both live, but either sex will remate if its mate disappears (E. L. Bull, pers. comm.).

Chronology of Courtship and Breeding

In Manitoba and Minnesota, great gray owls are mostly solitary in autumn and early winter, becoming increasingly gregarious toward March. Groups of up to 15 individuals have been observed in late winter (Nero 1980, J.R. Duncan, unpubl. data). Pair formation occurs as early as January and as late as 2 weeks prior to egg laying in April and May (Collins 1980, Franklin 1988). In Manitoba, courtship behavior and nest site inspections have been observed as early as November (Duncan 1987) but more typically in late February through April. In California, Oregon, and Manitoba, clutches are initiated as early as late March. Mean date of the first egg laid is 5 April in Manitoba (J.R. Duncan, unpubl. data) versus 5 May in Idaho and Wyoming. Egg laying is apparently delayed in years of heavy snow cover (Franklin 1988), and Bull *et al.* (1989b) observed earlier nesting in areas with lower snow cover. No second broods have been reported unless the first nesting attempt fails. One record of a renesting after 2-week old nestlings died is known (Bull and Henjum

1990). The timing of egg laying probably depends on the availability of prey (Voous 1988).

Only females develop a brood patch; and only females incubate, beginning with the first egg laid. Eggs are laid at 1 to 3-day intervals. Reported average incubation periods vary: 29.7 days (Idaho and Wyoming; Franklin 1988), 28-36 days (Scandinavia: Mikkola 1981), and 31 days in captivity (Ontario: K. McKeever, pers. comm.).

During incubation, females leave the nest only briefly and at long intervals to defecate and regurgitate pellets (Mikkola 1981, Bull and Henjum 1990). Males feed the incubating/brooding females and bring three to five prey per day to the female. Collins (1980) reports 0.27 feeding trips per hour by the male to the nest during the nestling stage in 135 hours of observation. Young great gray owls are fed at all times of day, but primarily around dawn and dusk.

Young either fall or jump from their nest at 3 to 4 weeks of age (Franklin 1988, Bull *et al.* 1989b). Owlets leave the nest over several days, with the oldest usually leaving first (Oeming 1955, Nero 1980, Bull and Henjum 1990). After leaving, young owls can readily climb leaning trees and roost off the ground. They can fly 7-14 days after leaving the nest (Franklin 1988).

Reported weights of juveniles just out of the nest range from 360 to 755 g. The mean weight at fledging was 507 g in Manitoba (Collins 1980, J. R. Duncan, unpubl. data) and 609 g in Oregon (Bull *et al.* 1989b). Females stay near their fledged young to protect them. After 3-6 weeks females abandon their young, but males continue to feed them for up to 3 months (Bull and Henjum 1990, Duncan 1992). Females may visit other adjacent family groups, occasionally returning to their own mate and progeny (Duncan 1987). Fledged young are known to join other fledged broods and may be fed by more than one male (J.R. Duncan, unpubl. data). Juveniles start hunting on their own at about 3 months, are independent by September/October, and disperse in late fall and winter.

Courtship Songs

Collins (1980), Nero (1980), and Winter (1986) describe vocalizations in North America. Cramp (1985) describes vocalizations of this species in Europe. Here we describe the dominant songs and calls that may be heard during surveys for this owl.

The territorial call given by both sexes is a repetitious series of low, evenly spaced *hoos*. Males have a lower pitch. This call is given most frequently during the pre-nesting season and while the male is near

a nest. It is audible for 400 m to 800 m (Cramp 1985). A second call of low, soft double hoots may be a contact call associated with defense of territory (Collins 1980, Nero 1980). A low, softer version of the territorial call is sometimes given by the male just before he delivers prey to the female. Another variation of *hoos* is given by the female when agitated, usually by human disturbance.

The repertoire of calls is greatest during the breeding season. Great gray owls are much less vocal when not breeding. An increase in vocal activity has been noted in autumn (J.R. Duncan, unpubl. data). The territorial call is primarily nocturnal. Winter (1986) found calling activity in California was greatest at 0100 hr, with a second peak at 2200 hr with 56% of calls heard between 0100 and 0400 hr. Calling declined conspicuously around midnight.

Parental Care

Only females incubate eggs and brood nestlings. After about 2-3 weeks, the female starts roosting near the nest. Males bring prey to the female and the female feeds the young. After fledging, the young are usually fed directly by the male. Owlets depend on adults until 130-160 days old. Few data document feeding rates at nests. Four young (> 14 days old) at a nest in Finland were fed, on average, 10.3 voles per day over 9 days (Pulliainen and Loisa in Cramp 1985). Females consume feces and pellets of their young until about a week before they fledge.

DEMOGRAPHY

Life History Characteristics

Nesting Success

Great gray owls rarely breed at 1 year, sometimes at 2 years, and more commonly at 3 years (Bull and Duncan 1993, J.R. Duncan, unpubl. data). One brood is produced per year. In 67 nesting attempts during 4 years in northeast Oregon, 78% fledged young (Bull *et al.* 1989b). In Idaho and Wyoming, 70.5% of nests fledged young (Franklin 1988); and in Manitoba and Minnesota 81% fledged (J.R. Duncan, unpubl. data). Of 427 Finnish nests, 95% hatched eggs and 69% fledged (Cramp 1985). Forty-two Finnish nests experienced 80.5% hatching success and 72.1% of chicks fledged. Fifty-eight percent of eggs survived to fledging.

Average clutch sizes in Europe vary from 0 to 4.6 eggs, seemingly in response to *Microtus* numbers (Mikkola 1983); Korpimäki (1986) cited a mean clutch size of 4.4 eggs. Mean clutch sizes reported in North

America are: 3 - 3.3 in Idaho and Wyoming (Franklin 1988); up to 5 in Oregon (Bull and Henjum 1990) and in Manitoba (Collins 1980); and 2 - 3 in California (J. Winter, pers. comm.). Mean number of fledged young per successful nest are 2.3 (SD = 0.87, range 1-5) in Oregon (Bull *et al.* 1989b), 2.7 - 3.0 (SD = 0.4, range 1-4) in Idaho and Wyoming (Franklin 1988), 2.8 in Manitoba (J.R. Duncan, unpubl. data), and 2.4 in Finland (Mikkola 1983). Producing 1.9-2.4 young per successful nest, great gray owls showed little annual variation in reproductive success during a 6-year Oregon study (Bull and Henjum 1990). In Scandinavia, however, Hilden and Helo (1981) reported fledging rates varying from 0 in poor prey years to 2.7 - 3.9 young/nest in good years. Twenty-one nests in Sweden fledged an average of 3.6 young/nest. No data establish lifetime reproductive success. In Manitoba, 91% of 32 radio-marked fledgling owls died before they were 1 year old (Duncan, unpublished data). Numbers of breeding owls corresponded with the number of *Microtus* in Canada but not to total numbers of small mammals or any other subgroup of prey (Duncan 1992). Non-dispersing adults died during population declines, but some individuals that had dispersed several hundred kilometers reproduced successfully. In Oregon, however, all radio-tagged adults nested each year (Bull *et al.* 1989b).

Survival

Franklin (1987) reported that a young great gray owl had a 63% chance of surviving from egg to flight stage; Mikkola (1983) reported a 58% chance. In Oregon, the probability of a juvenile surviving its first year is 53% and its first 2 years is 31% (Bull *et al.* 1989b). Annual probability of survival for nesting females in Oregon was 84% (95% confidence limit [CL] 70% - 100%) and for nesting males 91% (CL 78% - 100%) (Bull *et al.* 1989b). In Manitoba, 29% of 51 radio-marked adult owls (10 of 23 males and 5 of 28 females) died within 2 years (Duncan, unpublished data).

Individuals can be long lived. Cramp (1985) reported a 7-year-old owl and Oeming (1964) a wild 9-year-old bird. A female banded as an adult was recaptured 13 years later (R. W. Nero, pers. comm.). Korpimäki (1986) cited a life span of 11 years. In Canada, great gray owls failing to disperse following prey declines died over winter (Duncan 1992).

In Oregon, Manitoba, and Minnesota, avian predation accounts for most juvenile mortality (Bull and Duncan 1993). Starvation is also probably a significant cause of juvenile mortality but is difficult to quantify. Common raven (*Corvus corax*) predation

on eggs and young was significant in Oregon. Great horned owl predation on young and adults is reported from Manitoba and Oregon. Other reported sources of mortality include entanglement on barbed wire and electrocution on transmission lines. Collisions with automobiles are a major cause of mortality in some years (Nero and Copland 1981). Mikkola (1981) reported mortality of young resulting from mosquito and black fly bites.

Ecological Influences on Survival and Reproduction

Two principal factors appear to limit great gray owl populations through their influence on reproduction and survival: the availability of pre-existing nest sites and prey abundance/availability. Because great gray owls do not construct their own nests, factors affecting the availability of nest sites directly affect great gray owl breeding habitat. For example, outbreaks of certain insects can result in damaged tree tips or leaders. This damage can cause several tree branches in the whorl immediately below the lost leader to grow vigorously, creating a branch structure ideal for stick nests of hawks or ravens. Suppression of insect outbreaks may reduce the number of deformed trees and ultimately great gray owl nests. If successful, genetic improvements for trees used in plantations may lead to the same consequence. Pathogen resistance and selection for straight boles could reduce the number of trees suitable for primary platform nesting species.

Stick nests collapse after a few years of owl use. So, factors negatively affecting nest-building hawks and corvids may decrease productivity of great gray owl populations through a decline in available nest platforms. The availability of nest structures may fluctuate with cyclic prey populations of primary nest-building raptors. Patterns in great horned owl populations, which compete with great gray owls for nest platforms, will also influence nest availability.

Forestry practices that reduce the number of potential nest sites include the removal of diseased trees, removal of large trees, and forest stand alterations not compatible with the habitat requirements for nest-building species. Conversely, harvest prescriptions may increase nest site availability by altering habitat in a manner that favors primary nest building species, by promoting growth of large trees capable of supporting a large nest platform, or by leaving snag and snag replacements that will favor broken top nest structures.

Although many factors influence great gray owl survival, prey availability is thought to be a primary

factor. Despite of their large size, great gray owls prey almost exclusively on small mammals weighing less than 100 g. In the northern portion of their range, great gray owls depend on microtine rodents that exhibit multi-annual population fluctuations. When local prey populations crash, owls must disperse. Individuals that remain either starve or are predisposed to other mortality factors through decreased prey availability. Dispersing birds may experience increased mortality through increased risk of predation, accidents, or inadequate prey.

In the western United States, pocket gophers are thought to be an important buffer species allowing great gray owls to avoid nomadic movements. When vole populations decline, great gray populations may experience limited reproduction but can survive and remain resident on or close to their breeding home range. Pocket gophers, then, alter survival and movement patterns in these populations compared to northern populations. Gene flow and metapopulation structure are changed as a consequence.

Finally, annual mortality patterns in great gray owl populations are influenced by the abundance of raptors and prey available to those raptors. If raptors that occasionally prey upon great gray owls are abundant and their prey base declines, predation on great gray owls can be severe (Duncan 1987).

Social Pattern for Spacing

More research is needed on factors influencing territoriality, especially in relation to prey abundance. Adult males establish territories by vocalizing in the vicinity of the nest site (Bull and Duncan 1993). Territories can be established as early as the autumn prior to nesting (Duncan 1987). Given adequate prey, adult males in Manitoba and Minnesota may maintain a territory around the nest site all year (J.R. Duncan, unpubl. data).

Great gray owls appear to defend only the area immediately surrounding the nest site (Bull and Henjum 1987, Duncan 1987). Reid (1989) and Winter (pers. comm.) suggest that in California great gray owls defend foraging habitat, but the speculation is not based on thorough study of owl behavior. In other areas home ranges overlap (Servos 1986, Duncan 1987, Bull and Henjum 1990) and pairs readily nest within 0.5 km or less of each other (Nero 1980, Cramp 1985, Duncan 1987, Bull *et al.* 1988a). Duncan (1987) observed up to four adult males and their fledged young hunting in the same field. During the post-fledging period, adult females visit adjacent family groups (Duncan 1987).

Mikkola (1983) suggested that great gray owls may nest in loose colonies as short-eared owls (*Asio flammeus*) do and that they can be extremely tolerant of intraspecifics. The term "colony" may be a misnomer because the social unit likely does not function as a colony. Hoglund and Lansgren (1968) documented nests in Sweden as close as 100 m apart. In Finland, three nests were found within 400 m of one another (Mikkola 1976). Wahlstedt (1974) discovered seven pairs over a distance of 3 km in Sweden. Similar clusters of great gray owls have also been described by Duncan (1987) and Bull and Henjum (1990) in North America. An immature male was observed feeding a mated female brooding young while her mate, an adult male, was hunting 30 m away (Duncan 1987). Lower breeding densities may be more typical over the vast majority of its range.

Some observed agonistic encounters suggest winter territoriality, probably when prey are scarce (Brunton and Pittaway 1971, Nero 1980, J.R. Duncan, unpubl. data). Interpreting late winter behaviors, however, creates problems since they may be either agonistic or related to courtship.

Limiting Factors

Food supply likely regulates abundance of great gray owls in much of its range. When prey is scarce, many individuals abandon their breeding range. In one case, immediately after a prey decline in Canada, all non-dispersing birds died (Duncan 1992). In Oregon, all adult deaths occurred in fall and winter (Bull *et al.* 1989b). Although data suggest that prey availability influences great gray owl abundance in some areas, nest site availability likely limits owl abundance in other localities. Artificial nest sites allow breeders to settle new habitat. The relative importance of these factors in limiting population size has not been addressed. Geographic patterns in population limitation must be studied to provide a basis for conservation management.

Patterns of Dispersal of Young

The maximum distance that radio-tagged juveniles dispersed from natal sites in their first year ranged from 7.5 to 32 km in Oregon (Bull *et al.* 1988a). Two birds were found nesting 8.5 and 33 km from their natal site (Bull and Henjum 1990). In Manitoba, some immatures did not disperse from their natal site until March of the following year. Adults and juveniles travel much greater distances in the northern parts of their range; some to 753 km in Canada (Duncan

1992, see also the Movements section earlier in this chapter).

Characteristics of Non-Breeding Segment of Population

This important aspect of great gray owl population biology has not been studied, aside from the characteristics of pre-breeding individuals reported earlier.

Metapopulation Structure

In Oregon, great gray owls typically nest in the same home range year after year (Bull *et al.* 1989a). They will change nest sites but usually move < 5 km. Some birds in Oregon stay in the same area year round if snow is not deep; others move to areas with less snow. In Manitoba, some individuals returned to former nest sites after dispersing up to 500 km (Duncan 1992). Especially in the southern portion of the species' range, the demographic link between populations is provided by dispersing juveniles.

Because of the relatively continuous dispersion of suitable habitat throughout much of the species' range, great gray owls may not have a strong or well-defined metapopulation structure, as compared to the boreal owl for example (Hayward *et al.* 1993). The degree to which small populations of great gray owls in the Sierra, Cascade, or Rocky Mountains of the United States are separated from other local populations is unknown.

COMMUNITY ECOLOGY

Predators

Northern goshawks (*Accipiter gentilis*) and great horned owls frequently prey on juvenile great gray owls, particularly in years when grouse and hares are scarce (Nero 1980, Duncan 1987). Red-tailed hawks (*Buteo jamaicensis*) also attack juveniles (Bull and Henjum 1990). In Manitoba, juvenile owls were killed by black bear (*Ursus americanus*), fisher (*Martes pennanti*), and great horned owls (Duncan 1987). Adult birds are occasionally killed by Canada lynx (*Lynx canadensis*) and great horned owls (Duncan 1987, A. Franklin, pers. comm.).

The nest site is actively defended against common ravens, broad-winged hawks, northern goshawks, and great horned owls (Mikkola 1983, Bull and Duncan 1993, J.R. Duncan, unpubl. data). Intruders are chased and occasionally attacked. European ornithologists use a helmet and face mask when check-

ing nests. Mikkola (1983) reports several instances in which people without such protection suffered wounds or lost an eye to this species.

Competitors

Prey and nest sites likely limit great gray owl populations in various geographic settings. Great horned owl, broad-winged hawk, red-tailed hawk, northern goshawk, northern hawk owl (*Surnia ulula*), boreal owl, and long-eared owl nest sites have been found within 500 m of great gray owl nests (Lane and Duncan 1987, J.R. Duncan, unpubl. data; J. Winter, pers. comm.). The proximity of these nests, however, does not indicate that these species do not compete with great gray owls. Great horned owls are most likely to compete with great gray owls for nest sites since both species favor the open, abandoned nests of other large raptors (Nero 1980, Voous 1988). Potential exploitative competition for food among great gray owls and these raptors may exist because each consume small mammals from similar habitat.

Voous (1988) summarized the ecological relationships between this owl and others sharing its habitat. He indicated that, although the great gray owl is longer and larger in appearance than either the great horned owl in North America or the eagle owl (*Bubo bubo*) in the northwestern Palaearctic, its body mass is only 84% of the great horned owl's and 40% of the eagle owl's. Thus, despite its impressive size, the great gray owl takes relatively small prey and is unlikely to compete strongly with *Bubo* owls for food. Competition for food with long-eared owls, barred owls, northern hawk owls, and boreal owls is minimal or nonexistent during prey population highs, especially in northern regions. During prey population lows, however, competition is likely more important (Mikkola 1983, Johnsgard 1988).

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Dynamics of Forest Communities Used by Great Gray Owls

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INTRODUCTION

Great gray owls (*Strix nebulosa*) inhabit forests, but not all forests possess identical characteristics. To understand the owl, we must understand the dynamics of the vegetation communities that support them. Those dynamics operate differently in the Northern Rocky Mountains and the Cascade-Sierra Nevada complex, both of which are inhabited by great gray owls.

The range of the great gray owl in western North America south of Canada extends from northern California, Oregon, and Washington eastward through Idaho, Montana, and Wyoming. The owl's actual distribution in these states is irregular or even disjunct (Sanderson *et al.* 1980, Franklin 1988, Forsman and Bull 1989, Groves and Zehntner 1990, Bull and Henjum 1990, Bergeron *et al.* 1992). The great gray owl occurs wherever forests in these states meet their life needs, which not all forests do.

Pioneer ecologists C. Hart Merriam (1889) and Rexford Daubenmire (1943) were among the first to provide detailed ecological descriptions and interpretations of western forest zonation patterns. They also provided early understanding of how forest vegetation types in this region interacted with elements of the environmental complex: mountain physiography, geology, climate, wildlife, and wild-fire.

Modern ecologists have continued to accumulate knowledge on these complex interactions (Hall 1980a, Smith 1985, Habeck 1987, Peet 1988, Despain 1990). Interpreting the current status of owls in the Rocky Mountains (Franklin 1988) is predicated on accepting the idea that animals respond directly to (1) habitat features such as vegetation structure, vegetation composition, and forest patterns, and (2) successional stages following wildfire, cyclic insect and pathogen outbreaks, and silvicultural treatments (Thomas 1979).

Hall (1980b) made clear that any vegetation management aimed at enhancing native avian populations in western North American forests must be

based on understanding a given area's presettlement vegetation condition and the historically important processes that shaped it. Application of such baseline knowledge during the development and evaluation of forest management alternatives provides greater assurance of long-term avian management success (DeGraff 1980). Timber harvesting and altered natural fire regimes in the Northern Rocky Mountains will receive special attention in this analysis of vegetation dynamics.

NORTHERN ROCKY MOUNTAINS

The geographic area often designated as the Northern Rocky Mountains (NRM) extends from the Snake River Plain in southern Idaho, northward to the Canadian border. For this discussion I expand the area to include portions of western Wyoming and southeastern Idaho, encompassing Grand Teton and Yellowstone National Parks, and portions of the Caribou and Targhee National Forests, which are often included in the northern part of the Middle Rocky Mountains. All these places are areas of recent great gray owl studies and include the southern-most distribution of this owl in the Rockies (Franklin 1988, Groves and Zehntner 1990, Levine 1992).

Phytogeographic Provinces in the Northern Rocky Mountains

The low- and mid-elevation montane forests in the NRM used by the great gray owl fall primarily into USDA Forest Service's (1977) Western Forest Type #26, lodgepole pine (*Pinus contorta*) and Type #20, Douglas-fir (*Pseudotsuga menziesii*). Within Kuchler's (1964) potential natural vegetation types, the great gray owl's range falls within Type K-12, Douglas-fir, and Type K-15, Engelmann spruce-subalpine fir (*Picea engelmannii*-*Abies lasiocarpa*). The NRM region falls within Bailey's (1978) Highland Ecoregion, Rocky Mountain Forest Province, M3110, which features Douglas-fir.

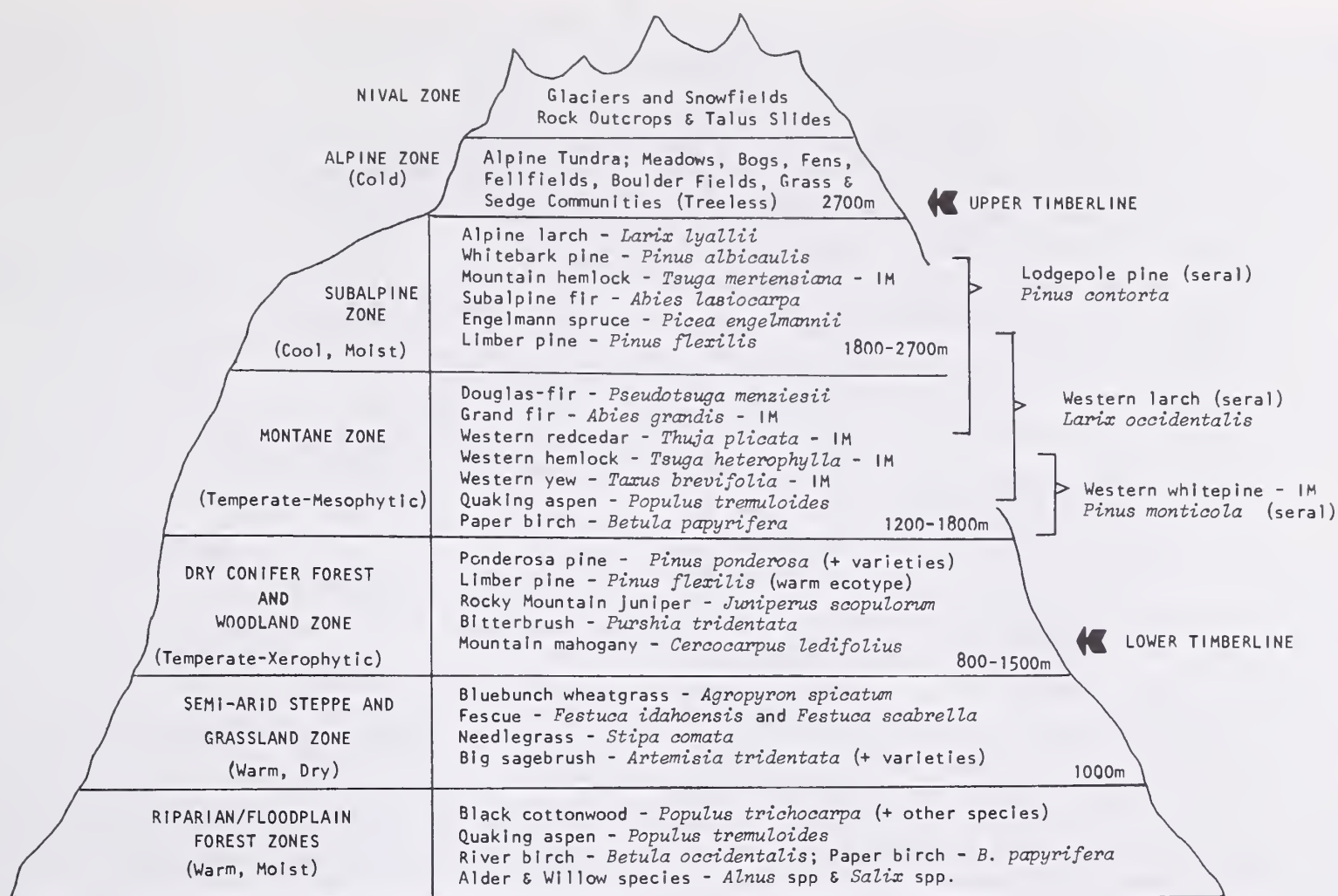


Figure 1.--Vegetation zonation in the Northern Rocky Mountains, typical of western Montana and northern Idaho. Approximate elevational limits of forest zones are given, as are average positions of upper and lower timberlines. Tree species functioning as post-fire seral dominants are shown on the right. IM = Inland Maritime Province (after Habeck 1987).

Rocky Mountain vegetation zonation has been graphically depicted in earlier reports by Habeck (1987) and are duplicated in figures 1 and 2. Peet (1988) summarized forest distribution patterns in the NRM through a series of gradient mosaic ordinations, wherein interactive elevation and moisture gradients are related to vegetation patterns (figures 3 and 4). Other graphic depictions of vegetation zonation and forest habitat type distributions for Montana, Idaho, and Wyoming are provided by Cooper *et al.* (1991), Pfister *et al.* (1977), Steele *et al.* (1981), and Steele *et al.* (1983). Despain (1990) has also provided graphic descriptions and interpretations of Yellowstone National Park (YNP) vegetation. Recent NRM vegetation reports usually include analyses of fire history and descriptions of post-disturbance forest succession.

In the northwestern NRM, south of Canada, including northeastern Washington, northern Idaho, and northwestern Montana eastward to the Continental Divide in Glacier Park, a moist inland-maritime subregion exists that features a well-developed oceanic (Pacific coastal) influence. Here the NRM exhibit nearly continuous forest cover composed of several conifers with west coast affinities. These include western red-cedar (*Thuja plicata*), western hem-

lock (*Tsuga heterophylla*), western white pine (*Pinus monticola*), and grand fir (*Abies grandis*). Forests dominated by these trees formed continuous cover before the era of logging. Before this century fires were less common in these moist forests with fire-free intervals of 100-200 years (Arno and Davis 1980). The only likely exception to the closed-canopy condition may have been natural lakes, marshes, and wet meadows occupying glacially formed depressions.

Elsewhere, away from the maritime influence, the remaining parts of the NRM experience significantly colder and drier continental climatic conditions. The latter areas display well-defined cold subalpine/timberline zones on the upper mountain slopes; these feature subalpine fir, Engelmann spruce, lodgepole pine, limber pine (*Pinus flexilis*), and white-bark pine (*P. albicaulis*). At lower elevations warmer, drier montane forests show a "lower timberline" composed of savanna, steppe, grassland, and shrubland types (Habeck 1987). The mid- to low-elevation montane forests are dominated either singularly or in mixtures of Douglas-fir, ponderosa pine (*Pinus ponderosa*), and lodgepole pine.

The several phytogeographic provinces composing the NRM (figure 5) were established by Arno

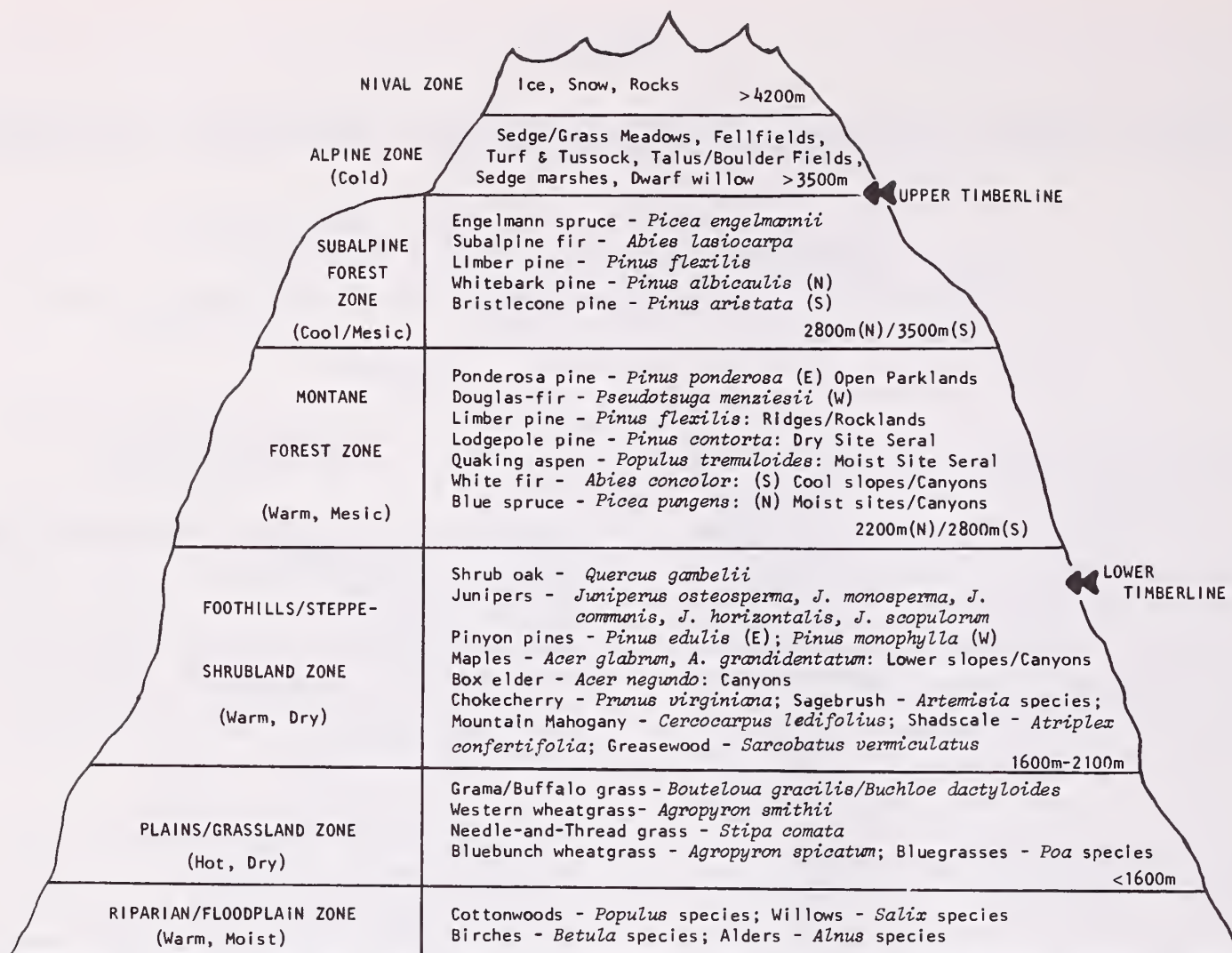


Figure 2.--Vegetation zonation in the Middle Rocky Mountains, typical of western Wyoming and central/southeastern Idaho. Positions of timberline are shown, and major dominants in each zone are listed. After Habeck (1987).

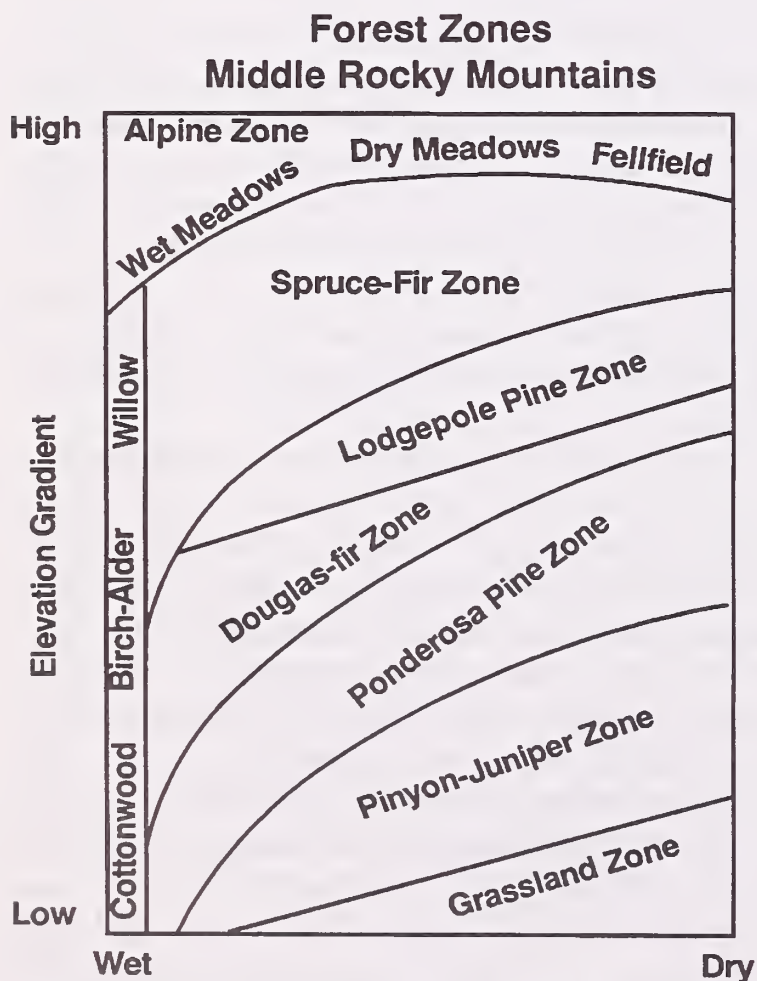


Figure 3.--Ordination diagram of Middle Rocky Mountain forest vegetation zones, including Yellowstone Ecosystem in western Wyoming and southeastern Idaho. Shown are topographic positions and limits of each forest zone employing elevation and moisture gradients as axes. Adapted after Peet (1988).

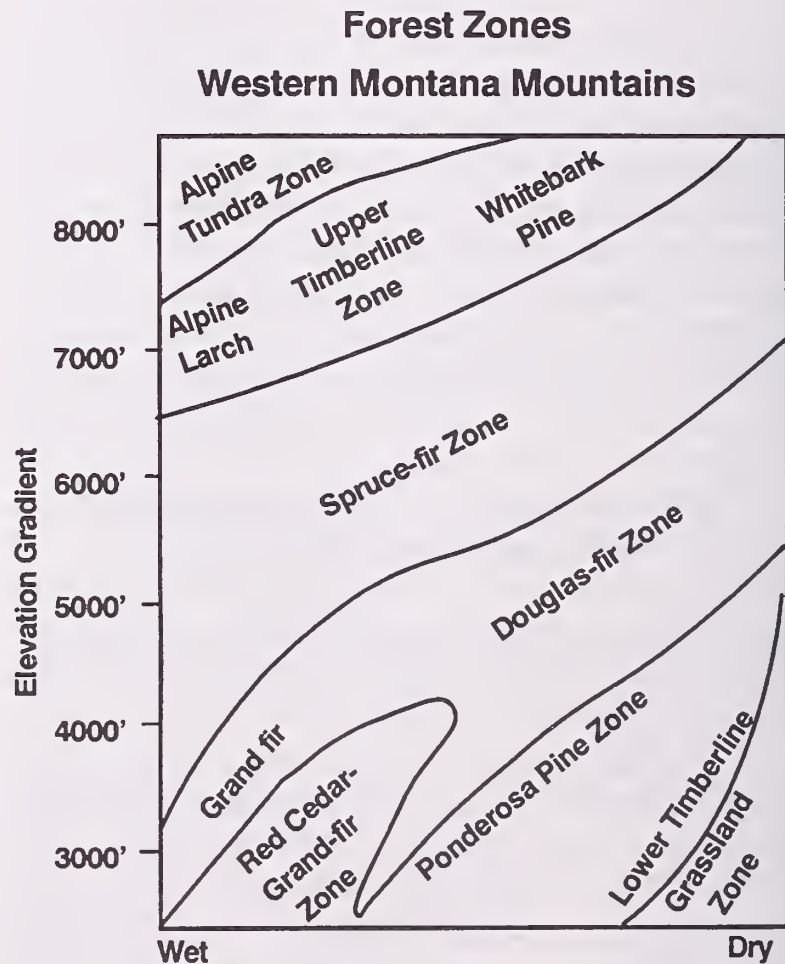


Figure 4.--Ordination diagram of western Montana forest vegetation zones, representing a major part of the Northern Rocky Mountains. Shown are topographic positions and limits of each forest zone employing elevation and moisture gradients as axes. Adapted after Peet (1988).

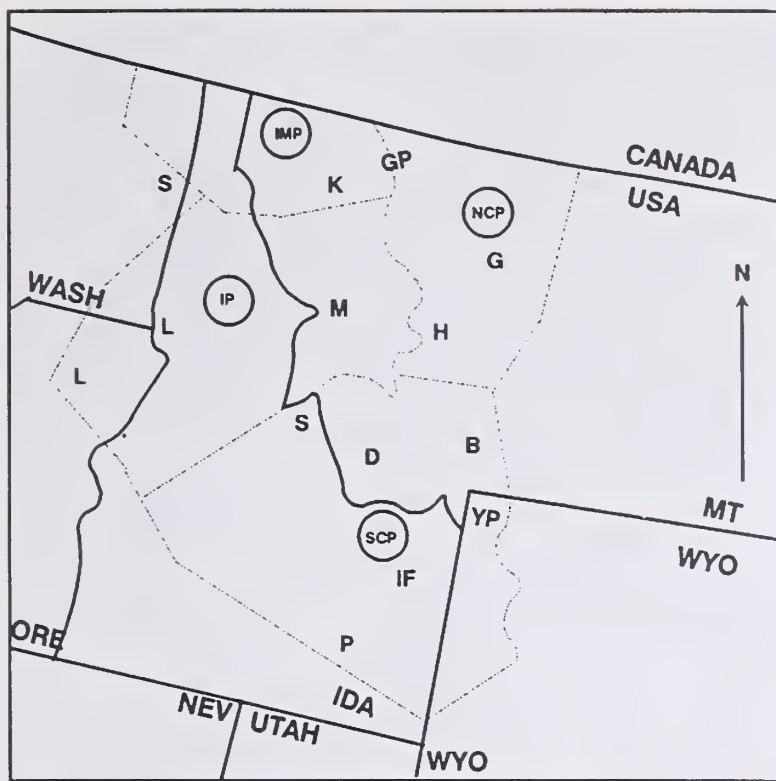


Figure 5.--Phytogeographic provinces (dot-dash lines) within the Northern Rocky Mountains. Shown are the limits of the Southern Continental Province (SCP), Northern Continental Province (NCP), Intermountain Province (IP), and Inland Maritime Province (IMP). Geographic points (letters) in Montana: M = Missoula, H = Helena, G = Great Falls, B = Butte, K = Kalispell, D = Dillon, GP = Glacier park; in Idaho: S = Salmon, L = Lewiston, P = Pocatello, IF = Idaho Falls; in Wyoming: YP = Yellowstone Park; in Oregon: L = La Grande; in Washington: S = Spokane. After Arno and Hammerly (1984) and Habeck (1987).

and Hammerly (1984). Each is differentiated by physiographic, climatic and floristic criteria. They provide a convenient outline of subregions for discussion of the NRM vegetation types that encompass the great gray owl's range. They include the Southern Continental Province (SCP), the Northern Continental Province (NCP), the Intermountain Province (IP), and the Inland Maritime Province (IMP).

Southern Continental Province

The Southern Continental Province includes those mountain ranges found in east-central Idaho and southwestern Montana: Sawtooth Mountains, Lost River Range, Lemhi Range, Beaverhead Range, Gravelly Range, and Madison Range. Contiguous to these, in west-central Wyoming and southeastern Idaho, are the Teton Range, Snake Range, Caribou Range, and Wasatch Range. The montane zones in this province are dry and cool, the low moisture (20-40 cm annually) is a result of a rainshadow partly induced by the Cascade, Blue, and Wallowa Mountains to the west in Oregon, and mountain ranges in Idaho. Forest cover in SCP ranges is generally confined to a relatively narrow zone between lower timberline at 2000 m and upper timberline at 2700 m.

Ponderosa pine is not well represented in the lower forested zones in SCP because of the cold climate and short growing season at lower timberline (Arno and Hammerly 1984). Instead, Douglas-fir is the common dominant tree adjacent to the steppe-grassland zone (*Artemisia/Agropyron-Festuca* dominated). Limber pine found in both upper and lower timberline forests joins Engelmann spruce in defining the upper timberline of dry mountain ranges. In ranges with greater moisture, Engelmann spruce typically combines with subalpine fir and white-bark pine.

Almost all forested portions of western Wyoming, Idaho, and Montana routinely burned before 1900 (Wellner 1970, Habeck and Mutch 1973, Gruell 1985a, 1985b, Bradley *et al.* 1992, Losensky 1993). As the 20th century began, lodgepole pine dominated NRM seral forest communities, covering valleys and slopes to upper timberline (figure 6). Presettlement fires occurred at various intervals. Northern Yellowstone National Park burned every 20-25 years, usually at low intensities, creeping sporadically through the forests, consuming surface litter and seedlings of climax tree species, and maintaining open forest canopies. Near Jackson Hole, south of YNP, fire-free periods lasted 80-100 years, and south and east of these areas fire frequencies may have been even less (Gruell 1980, Steele *et al.* 1983, Despain and Romme 1991).

The Yellowstone Plateau has been forested over the past century with a relatively uniform expanse of lodgepole pine, with scattered-to-dense pockets of white-bark pine. On sites protected from fire for several centuries, old forest stands of subalpine fir and Engelmann spruce prevail (Steele *et al.* 1983, Bradley *et al.* 1992). In the Jackson Hole region historic fires perpetuated lodgepole pine and quaking aspen (*Populus tremuloides*). Much of YNP falls into subalpine fir habitat types (potential climax), but fires have perpetuated lodgepole pine as a major seral dominant in the park (Despain 1990, Despain and Romme 1991). Peet (1988) describes lodgepole pine as the "archetypal post-fire species." Although many lodgepole pine become established immediately after a fire, its serotinous cones shedding abundant seeds, lodgepole pine apparently continues establishing itself over a 30-50 year period or longer. The percentage of cone serotiny among lodgepole pine populations varies in relation to the specific mode of stand establishment and whether recovery follows fire or other types of disturbance, such as blowdown or insect damage (Lotan and Perry 1983). Quaking aspen is well known for its vegetative resprouting after being burned, but the 1988 YNP fires were followed by extensive sexual reproduction of aspen (Kay 1993).



Figure 6.--Old lodgepole pine forest, with *Pinus contorta* and subalpine fir reproduction in understory. Stand located on Main Bear Creek, Gardner District, Gallatin National Forest, Montana, Southern Continental Province (see text). This type of mature lodgepole pine forest community is widespread throughout the Yellowstone Ecosystem in Montana, Wyoming, and Idaho. Photo by Danny On, September 1966, USDA Forest Service photo.

Fire exclusion policies implemented after 1900, climatic changes (cyclic drought), and livestock grazing have all been identified as factors contributing to the successional invasion of conifers into lodgepole pine/steppe grassland community types occupying the montane zones of SCP mountain ranges (Gruell 1980, Arno and Gruell 1983, Habeck 1987, Bradley *et al.* 1992). In 1886, a total of 22 million cattle grazed western North American ranges, and sheep numbered over 15 million in Montana, Idaho and Wyoming at the turn of the century (Stewart 1936).

Before 1900 wildfires regularly killed invading conifer seedlings and saplings. Extensive and intensive livestock grazing reduced fine fuel loadings and altered grass-conifer competition (Bradley *et al.* 1992). After many decades of fire exclusion, upper elevation seral lodgepole pine and Douglas-fir stands usually become invaded by shade-tolerant subalpine fir, or sometimes by Engelmann spruce (Peet 1988). Higher fuel loadings now exist, leading to a greater potential for high intensity fires over much of the Northern Rockies.

The Greater Yellowstone Area (GYA), including parts of SCP in Idaho, harbor several native (endemic) insect species that periodically reach epidemic population levels (Despain 1990, Ammon and Ryan 1991). Western spruce budworm (*Choristoneura occidentalis*) had killed numerous Douglas-fir in YNP stands, and mountain pine beetle (*Dendroctonus ponderosae*) has a long history of widespread killing of white-bark pine and lodgepole pine in this part of the Rockies. Cyclical insect outbreaks, spanning a decade or more, are closely correlated with episodes of drought, and have led to extensive conifer mortality in GYA and elsewhere in the Rocky Mountains. Despain (1990) discusses the possible interactions between mountain pine beetles, mature-sized lodgepole pine, and fire. Insect-killed timber does provide increased fuel, but insect-killed mature pines may be less capable, according to Despain, of supporting rapid-spreading crown fires than are smaller living trees. Without fire the insect-killed forests undergo succession involving the potential climax subalpine fir and/or Engelmann spruce.

Dwarf mistletoe (*Arceuthobium* spp.) infestations also cause a significant build-up of dead, woody fuel on the forest floor and witches'-brooms in the tree canopies, setting the stage for intense wildfires (Crane and Fischer 1986). These latter authors have established a series of "fire groups" for central Idaho that have application elsewhere in the SCP. They have generated a series of post-fire forest successional pathway models for forest habitat types common in central Idaho. Wildlife responses to fire treat-

ments in each "fire group" are also documented by Crane and Fischer (1986) and Bradley *et al.* (1992).

Wind and snow breakage are less common, but nevertheless influential forces acting on SCP forest communities. Tornado-level winds or severe thunderstorm down drafts ("microbursts") can cause extensive areas (100-300 ha) of broken stems and blowdowns of criss-crossed tree stems. If fire does not intervene, post-wind succession is usually rapid, involving only a minimum of compositional change.

According to Steele *et al.* (1983), the eastern Idaho-western Wyoming portion of the SCP experienced intensive early-day logging at lower elevations where timber was most accessible to town sites, homesteads, and mining developments. Usually only high quality timber was selectively taken. Transcontinental railroad construction created a demand for track ties which were taken from tie-sized members of Douglas-fir and lodgepole pine populations occupying lower elevations (Steele *et al.* 1983). This latter type of "tie-hacking" selection left size/age class gaps in forest tree populations which Steele *et al.* (1983) found detectable in their modern forest surveys. Steele *et al.* (1981), discussing central Idaho forests, state that recovery from logging disturbance is very slow, and the "clearcut and burn" techniques used in northern Idaho and western Montana failed as tree regeneration techniques in the more droughty and nutrient-stressed sites found in central Idaho. Modern logging still focuses on the most accessible forest stands. Only the steep, rugged mountain terrain prevents the removal of remnant old forests remaining in SCP mountain ranges. National parks and designated wildernesses in this subregion of the Rockies still support a reasonably complete size and age array of forest types, but even collectively they represent only a restricted acreage (Steele *et al.* 1981).

Unregulated cattle grazing during 1860-1900 (Stewart 1936) impacted substantial portions of SCP. Livestock damage was greatest in parts of the forest where grasslands and meadows interrupt the forest cover. New clearcuts cause localized congregations of cattle, and conifer seedlings are killed by trampling. More importantly, exotic plants are now replacing native grasses and forbs. Since 1900 regulation of livestock grazing has increased, but recovery from past disturbance is slow and of variable success. Wildfires, logging, insect and disease outbreaks, as well as other factors appear to have maintained much of SCP's forest cover in various stages of successional recovery. Very little of the landscape supports mature seral or climax old growth forest (Steele *et al.* 1981, 1983).

Few current studies from SCP specifically cite old-



Figure 7.--Old-growth *Pinus contorta* forest with scattered snags (background), adjacent to "temporary meadow" (foreground) created by clear cutting. This landscape combination of old-growth lodgepole pine forest and contiguous clearcut sites provides suitable nesting and foraging habitats for *Strix nebulosa*. Area located on the Bozeman District, Gallatin National Forest, Montana W. E. Steuerwald, August 1964, USDA Forest Service photo.

growth, perhaps because of the reduced amounts of these forest types. Mehl (1992) provides old-growth descriptions for the Middle Rocky Mountains, including Wyoming. He makes clear that older forests dominated by fire-dependent species, such as mature seral lodgepole pine, or by shade tolerant climax species, such as subalpine fir, are encompassed within current old-growth classifications. Mehl summarizes stand characteristics and attributes that have been used to develop old-growth definitions in the Rocky Mountains, and these definitions are currently being used to inventory remaining old-growth. Of further significance, in relation to the great gray owl's habitat requirements, Mehl points out that as old-growth stands continue to mature in the absence of stand-altering disturbances, canopy gaps are formed following tree death and downfall. Such canopy openings enhance the great gray owl's flight movements through stands where nest sites exist.

Levine's (1992) great gray owl surveys were concentrated in the Wasatch Range in southeastern Idaho, the southern reaches of the Rockies considered within the SCP. This region closely coincides

with the great gray owl's southern distributional limits. The Wasatch Range is exceptionally steep and rugged and represents the western edge of the Rockies (Arno and Hammerly 1984); its peaks reach up to 3600 m. Upper timberline consists of Engelmann spruce, subalpine fir and limber pine, with all of these exhibiting krummholz life forms. Pacific storms bring considerable winter and spring snowfall, which produces frequent snow avalanches that cut through subalpine and montane forest zones.

Gruell (1980) summarized the influence of reduced fire frequency on wildlife habitat in Bridger-Teton N.F., Wyoming, adjacent to Caribou N.F. where lodgepole pine stands now lie between valley floor and 2700 m. He stated that lodgepole pine stands have changed considerably over the past century. Subalpine fir has become a principal component in the understories of lodgepole forests. Subalpine fir has also been invading mature fire-generated Douglas-fir in this part of the SCP.

Levine (1992) noted that the average elevation where great gray owls were found was at 2276 m (range 2194-2378 m on lower to middle north-slope aspects). Forests at this elevation are late seral or

mature mixed stands dominated by lodgepole pine, either unlogged or only partially cut, with 70-90% canopy closure. Owls were not noted in other forest types in this part of the Wasatch Range. All owl locations were adjacent to riparian meadows, other wetlands, or clearcut sites. Figure 7 illustrates the combination of old lodgepole pine forest and a contiguous clearcut site at the northern end of the GYA.

Northern Continental Province

The Northern Continental Province (NCP) includes mountain ranges in central Montana, east of the Continental Divide ("Rocky Mountain Front"): Lewis Range, Big Belt Mountains, Crazy Mountains, Little Belt Mountains, Bear Paw Mountains, and Sweetgrass Hills (figure 5). Great gray owl sightings, including evidence of successful breeding, have been made in the Lewis and Clark N.F. and Deerlodge N.F., both located in NCP. Mature lodgepole pine forests surrounding, or adjacent to natural meadows compose the landscapes where these sightings occurred (Montana Natural Heritage 1993 Database, Bergeron *et al.* 1992). Circumstantial evidence of breeding owls as well as simple observations are recorded over a broad range of NCP.

Valley elevations in NCP are lower than within SCP, and somewhat less arid than SCP. Lower timberline is 1200-1500 m, and continuous forest cover occupies a broader elevational range than in SCP. Ponderosa pine forms the lower timberline in this part of the Montana Rockies. However, ponderosa

pine does not tolerate fluctuating winter temperatures, so, north of Great Falls, it is replaced by combinations of quaking aspen, Douglas-fir, limber pine, and lodgepole pine (Arno and Hammerly 1984).

USDA Forest Service Forest Type #20, Douglas-fir, Type #21, ponderosa pine; and Type #26, lodgepole pine, compose much of the conifer forest cover in NCP (1977). Kuchler's (1964) potential natural vegetation forest types for the same province include K-11 and K-16, ponderosa pine; K-12, *Pseudotsuga*; K-15, *Picea-Abies*; and K-98, *Populus-Salix*. The latter floodplain forest type occupies riparian sites on the Missouri and Yellowstone Rivers. Large expanses of NCP are covered with K-63, *Agropyron-Festuca-Stipa* (Foothills Prairie) and K-64, *Bouteloua-Stipa-Agropyron* (Grama-Needlegrass-Wheatgrass). The montane zones (1500-1800 m) of NCP mountain ranges are dominated by varying mixtures of Douglas-fir and lodgepole pine. The upper zones are codominated by subalpine fir, Engelmann spruce and white-bark pine. Upper timberline occurs between 2300 and 2600 m.

As a part of the effort to implement ecosystem management in the northern Rockies, Losensky (1993) analyzed early forest inventory records and used these records to describe the historic forest vegetation throughout the Forest Service's Northern Region, including NCP. Timber resources came under heavy use soon after gold discovery in the 1860s. Ranching and agricultural development between 1880 and 1900 further reduced forest cover. Else-

Table 1.—Percent of acres, by age classes and forest cover types for Northern Region (R1) National Forest lands, including northern Idaho and western Montana, circa 1900. Data are projections from a historic vegetation map and early-day timber inventories compiled and analyzed by Losensky (1993).

Forest type	Non-stocked acres	Seedlings & saplings 1-40 yr	Pole stands 41-60 yr	Immature stands 61-101 yr	Mature stands 101+ yrs	Potential old forest 121+ yrs
White pine	21%	23%	4%	10%	17%	25%
Ponderosa pine	10	9	4	5	24	48
Larch/	19	24	6	9	17	25
Douglas-fir						
Hemlock/	3	10	13	4	26	44
Grand fir						
Douglas-fir	22	20	7	18	26	7
Engelmann spruce	7	8	2	10	32	41
Lodgepole pine	25	41	9	15	7	3
Redcedar	7	7	1	8	6	71
Cedar/	15	16	17	10	18	24
Grand fir						
Average for all types	17%	23%	6%	12%	17%	25%

where on the Rocky Mountain Front, construction of the Great Northern Railway in 1892 led to the harvesting of significant amounts of timber. Railway construction also triggered a period of increased fires within forests adjacent to the rights-of-way. Losensky's summary of historic forest inventory data (age class per cover type for 1900 data, and volume per cover type for 1930's data; national forest lands only) for northern Idaho and western Montana, are presented in tables 1-2. These data are being used as reference points to assess shifts and alterations that have taken place in the Northern Rocky Mountains over the past 60-100 years (table 3).

Fire played a major role in forest dynamics throughout the East Front of the Montana Rockies; an in-depth analysis of fire ecology east of the Continental Divide is provided by Fischer and Clayton (1983). They established a series of "fire groups" to organize and discuss the ecological role of fire within forest habitat types found in an area that closely matches the geographic extent of the NCP. Some of these groups feature ponderosa pine occupying warm-dry sites as well as warm-moist sites. Similar treatment is given to Douglas-fir habitats on a range of sites. One fire group is assigned to lodgepole pine stands that were historically perpetuated by periodic fires.

Ponderosa pine resists fire well. Even seedlings and saplings of this species can withstand high temperatures generated by surface fires or from the thermal stress associated with hot, dry exposures. On

Table 2.—Percentage area by cover type for USDA Forest Service Northern Region (R1) federal forest lands in northern Idaho and western Montana, based on timber inventories conducted in 1933; data compiled by Losensky (1993).

Forest cover type	Northern Idaho forests	Western Montana Forests
Western white pine	22.4	2.0
Ponderosa pine	13.0	13.7
Larch/Douglas-fir	9.1	17.3
Hemlock/grand fir	1.7	0.1
Douglas-fir	5.9	5.1
Engelmann spruce	2.1	2.3
Lodgepole pine	8.1	13.4
Western redcedar	0.4	0.1
Redcedar/grand fir	1.8	Trace
Spruce/subalpine fir	10.7	12.9
Noncommercial forests	7.3	15.5
Nonforest	17.5	17.6
Totals	100.0	100.0

Table 3.—Changes in historic land cover and vegetation type groups in USDA Forest Service's Northern Region (R1) occupying all federal lands in Idaho, Montana, and portions of the Dakotas, based on a draft assessment of data originating from a 1933 historic vegetation map (Losensky 1993) and a 1993 NDVI (Normalized Difference Vegetation Index) vegetation index map displaying existing vegetation cover classes (Hann *et al.* 1993). Vegetation types created by agricultural tilling and woodlots added as new 1993 categories. MM = millions of acres.

Land cover/ vegetation type groups	Historic vegetation acres (MM) (1933)	NDVI vegetation acres (MM) (1993)
Lodgepole pine	8.5	11.5
Spruce/subalpine fir	2.3	1.7
Douglas fir	7.7	9.3
Western larch/Douglas-fir	3.2	1.1
Western whitepine	3.0	0.2
Ponderosa pine forest	6.5	12.5
Ponderosa pine savanna	2.8	0.3
Douglas-fir savanna	0.6	1.5
Wheatgrass/fescue	22.2	1.1
Sagebrush/grassland	3.4	10.1
Mixed-grass prairie	83.7	53.6
Tall-grass prairie	22.7	0.6
Hardwood riparian	7.0	2.1
Oak savanna	0.9	0.1
Alpine zone	0.1	0.4
Woodlots	0.0	2.1
Agriculture crops	0.0	69.8
Water	0.6	1.0

dry sites historic fires maintained open canopies with grassland understories; crown fires were rare. On more moist sites, however, ponderosa pine formed two-storied canopies which were susceptible to higher intensity crown fires. Douglas-fir is only moderately fire-resistant, and Douglas-fir reproduction is very vulnerable to even low-intensity surface fires. When individual Douglas-firs achieve larger sizes, they develop thick, protective bark which allows them to survive underburning. During the past half century, dense sapling thickets have developed, forming ladder fuels that now endanger the crowns of old-growth Douglas-fir (Habeck 1990).

Generally lodgepole pine's relatively thin bark makes this species susceptible to lethal cambium heating. Individual, mature lodgepole pines, however, do display moderate resistance to surface fires. Throughout NCP lodgepole pine displays cone serotiny (resin-sealed scales), which assures a continued population even in the presence of frequent wildfires. Some lodgepole stands that became established after fires are so dense they are susceptible to

stagnation, snow breakage, windthrow, disease and insect infestations, all of which combine to set the stage for a high-intensity, stand-replacing fire (Lotan and Perry 1983).

Up to the mid-1970s about 50% of forested lands in Montana had been logged (Pfister *et al.* 1977). The percentage may be even higher in the NCP because of extensive historic use of timber for mining operations and railway construction between 1870 and 1920. Some forested tracts in the vicinity of Butte (Highland Mountains mining district), for example, were logged nearly to alpine timberline. Furthermore, modern fire suppression (post-1900) led to extensive forest encroachment into mountain grasslands (Arno and Gruell 1983, 1986).

Studies of the historic importance of fire on forest vegetation in the Deerlodge National Forest (Habeck 1992) have shown how the conifer invasion sequence progresses. Fire-maintained, open-canopied old Douglas-fir communities have become densely stocked and grassland species have declined from the forest understories. The 400+ year-old Douglas-firs, completely surrounded by the invading conifer reproduction, are now in danger of being killed in the next wildfire. As a consequence, loss of remaining old Douglas-fir forest is possible. A pilot landscape analysis was recently completed in a portion of NCP, aimed at integrated resource planning (O'Hara *et al.* 1993). The report discussed the historical importance of fire in the mixed conifer forests (subalpine fir, lodgepole pine and Douglas-fir) located in the NCP (Elkhorns Landscape Analysis Area, Helena N.F.) This analysis further confirmed the declining extent of mountain meadow grasslands in NCP as a result of modern fire control. The potential loss of old coniferous forests as well as reduced grasslands has direct implication to the maintenance of great gray owl's nesting and foraging habitats in this Rocky Mountain subregion.

Intermountain Province

The Intermountain Province (IP) includes north-eastern Oregon, central Idaho and west-central Montana (figure 5). The Blue and Wallowa Mountains are found in northeastern Oregon; the Clearwater Mountains, Salmon River Mountains, and the western edge of the Bitterroot Mountains occur in Idaho; the Sapphire Range, Anaconda-Pintler Range, Flint Creek Range, and the southern extensions of the Mission and Swan Ranges are located in westcentral Montana.

Bull and Henjum (1990) documented numerous great gray owl breeding sites in northeastern Oregon conifer forests. In this region great gray owls com-

monly use abandoned raptor stick nests in mature western larch (*Larix occidentalis*), with some located in Douglas-fir. Mature ponderosa pine and Douglas-fir are often used as perch trees within nearby meadows and clearcuts serving as foraging sites. Atkinson (1989) reported breeding great gray owls on the Payette N.F. in central Idaho. His studies showed that mature, mixed conifer forests, dominated by Douglas-fir and/or grand fir, exhibiting high snag densities, and bordering natural meadows or small clearcuts, were commonly associated with his great gray owl sightings.

Great gray owl sightings, plus direct and indirect evidence of breeding great gray owls have been reported for an assortment of low to mid-elevation montane forests in western and northwestern Montana (Montana Natural Heritage Program Database 1993). In western Montana mature lodgepole pine and old-growth western larch forests (figure 8) are commonly associated with great gray owl occurrences. The presence of late seral stands dominated by fire-dependent lodgepole pine and western larch in montane forests (1200-1800 m) in the IP is closely correlated with historic wildfire (Arno 1980, Habeck 1987, 1990). Repeated (50-100 year intervals) fires maintained a landscape fire mosaic wherein the disturbance-dependent lodgepole pine and western larch were major components. Modern fire suppression and logging throughout IP shifted the fire mosaic from presettlement conditions and changed the environment of the great gray owl.

Intermountain Ranges are partially influenced by moist maritime air masses that pass nearby, but they receive less total moisture than does the Inland Maritime Province (IMP) to the north; summer months are typically dry. The more severe continental climate that features temperature extremes, plus cold, dry winters, and stressful chinook winds is not commonly expressed in the IP subregion (Arno and Hammerly 1984, Habeck 1987).

The montane forests of IP serving as owl habitat fall within Forest Service (1977) Type #20, Douglas-fir; Type #21, ponderosa pine; Type #26, lodgepole pine; Type #25, western larch; and Type #23, subalpine fir/Engelmann spruce. Kuchler (1964) forest types include K-11, ponderosa pine; K-12, Douglas-fir; K-14, grand fir/Douglas-fir; and K-15, Engelmann spruce/subalpine fir. Bailey's (1978) Ecoregions represented in IP include M3111, M3112 and 3120 (bunchgrass/wheatgrass-needlegrass Types), and M2112 (cedar/hemlock/Douglas-fir).

Intermountain province forest habitat type classifications by Pfister *et al.* (1977), Mueggler and Stewart (1980), Cooper *et al.* (1991), Steele and Geier-



Figure 8.--Old-growth *Larix occidentalis* forest, with Douglas-fir and subalpine fir in understory. Note broken-topped snags and mistletoe-infected "witch's-brooms," both of which may serve as *Strix nebulosa* nest sites. Open, wet meadows, filling glaciated depressions occur on nearby sites. Great gray owl sightings have been recorded in this area. Condon District, Flathead National Forest, Montana, within the Intermountain Province. Danny On, October 1965, USDA Forest Service photo.

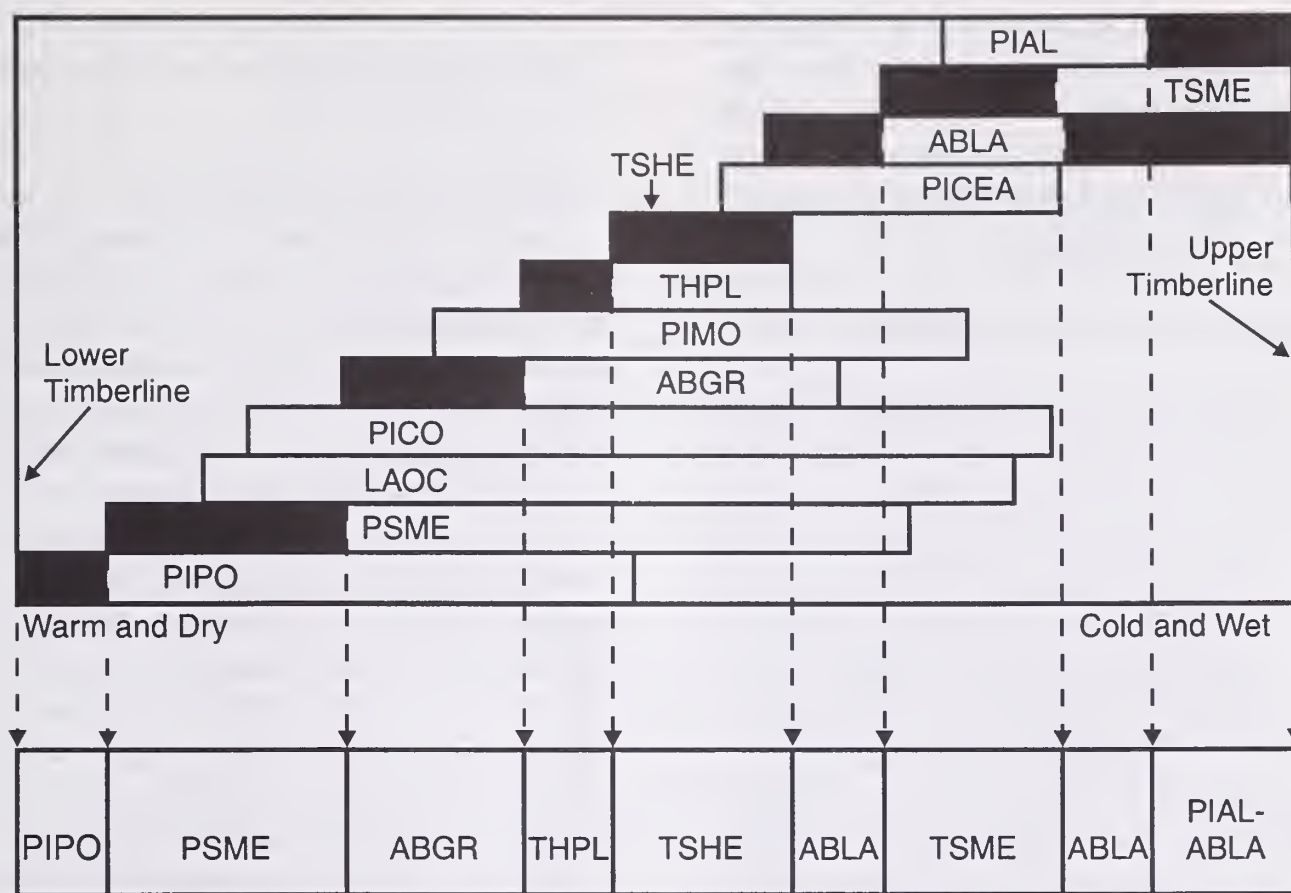


Figure 9.--Schematic distribution of conifers in Montana portion of Rocky Mountains, arranged vertically, showing usual order in which trees are encountered with increasing elevation. Horizontal bars designate upper and lower limits of each tree species compared to climatic gradient. Black areas represent portions of elevational range where each shade-tolerant species exhibits climax characteristics; the climax species are identified on the lower graph. PIPO = ponderosa pine, PSME = Douglas-fir, LAOC = *Larix occidentalis*, PICO = *Pinus contorta*, ABGR = *Abies grandis*, PIMO = *Pinus monticola*, THPL = *Thuja plicata*, TSHE = *Tsuga heterophylla*, PICEA = *Picea engelmannii*, ABLA = *Abies lasiocarpa*, TSME = *Tsuga mertensiana*, PIAL = *Pinus albicaulis*. Adapted after Green et al. (1985).

Hayes (1992), provide summarized information on vegetation distribution patterns (zonations). An example is shown in figure 9. Vegetation cover occurring in northeastern Oregon and southeastern Washington are reviewed by Franklin and Dyrness (1973), and Hall (1973, 1980b). Johnson and Clausnitzer (1992) have published a revised classification of the vegetation in the Blue and Ochoco Mountains in Oregon. The role of fire in IP forest types has been addressed in Hall (1980a), Crane and Fischer (1986), Fischer and Bradley (1987), and Walstad *et al.* (1990).

The mountain ranges in IP have well-defined lower and upper timberlines. In pre-settlement times the lower timberline (800-1500 m) was impacted by frequent (10-30 year intervals), low intensity fires ignited by lightning and native Americans (Barrett and Arno 1982, Gruell 1983, 1985a, 1985b, Habeck 1990). Pre-1900 burning perpetuated grasslands and ponderosa pine savannas. This seems true even on mesic-moist sites where Douglas-fir and/or grand fir are the potential climax dominants. After the horse was acquired by American Indians occupying the northern Rockies (1730's), extensive Indian burning for pasture production is likely to have converted mesic montane forests to savanna or grasslands (Habeck 1990). Open park-like stands of old Douglas-fir and ponderosa pine forests were per-

petuated by fires throughout IP montane zones (Habeck 1987).

Above the ponderosa pine zone lies the Douglas-fir/grand fir forest zone, extending from 1200-1800 m. Within this zone western larch often prevailed, historically, as a major seral species. This fire-dependent tree often lives 400-500 years, and may achieve diameters of 1.0-1.5 m, and heights over 40 m.

Within the IP subalpine fir dominates the zone between 1800 m and treeline at 2700 m; lodgepole pine extends into this zone and mixes with white-bark pine and Engelmann spruce. Historic wildfires also occurred in this higher forest zone, but intervals between fires were usually more than 100 years, not uncommonly 200-300 years. Some grassland communities dominated by *Agropyron spicatum*, *Festuca scabrella* and *F. idahoensis*, occurred within the IP's montane and subalpine forests. Subalpine meadows dominated by green fescue (*Festuca viridula*) and surrounded by white-bark pine were very common at timberline (2700 m) in northeastern Oregon and west-central Idaho before settlement. Intensive sheep grazing in the early 1900s severely damaged these meadow habitats (Arno and Hammerly 1984); they are now recovering following reduced grazing pressure.

Perhaps the most widespread loss on IP land-

scapes, attributable to logging and post-1900 fire suppression, has been the disappearance of ponderosa pine woodlands in the lower montane zones. As elsewhere in the Northern Rockies, centers of mining activity were the first areas to be heavily logged (Cooper *et al.* 1991). The wood needs for mine timbers, railroad ties, fuel, and building material, as well as clearing for agriculture led to massive forest clearing in IP.

Hutchinson and Winters (1942) compiled a forest resources inventory for northern Idaho that emphasized the heavy removal of western white pine a half century ago. The allowable annual cut of western white pine in 1941 had been established to be 140 million board feet (mm db ft), reflecting a level of white pine harvest that fit a system of sustain-yield forestry. However, they reported that during an earlier four year span (1935-38), western white pine was subjected to an average annual cut of 351 mm db ft! Other conifer species were essentially ignored during this period. This disproportionate cutting of old-growth white pine in northern Idaho strongly impacted this area's forest landscape including the wildlife it supported. The post-World War II building boom accelerated timber harvesting further, especially in the lower and montane zones. On the Clearwater N. F. in Idaho, for example, the annual cut expanded from a high of 18.0 mm bd ft prior to 1946, to 116 mm bd ft by 1959, with similar jumps in other regional forests. Much of this log removal focused on harvesting old growth. See Losensky's (1993) historic forest inventory data, tables 1 and 2).

The belief that the lower montane forests in the Northern Rockies have been changed the most by modern man's influence has also been expressed by scientists contributing to the 1993 Forest Ecosystem Health Assessment Report (Jensen and Bourgeron 1993). Elsewhere, in other IP fire-adapted ecosystems such as in central Idaho and northeastern Oregon, reduced natural fire, increased selective logging of mature late-seral trees, continued livestock grazing, and cyclic drought have collectively disrupted natural forest functions.

Present-day influences have led to epidemic levels of insect infestations (Carlson and McCaughey 1982, McCune 1983) followed by unnatural, high-intensity wildfires degrading overall ecosystem health (Mutch *et al.* 1993). These circumstances have implications to avian habitat management and will require innovative silvicultural strategies to reverse the present trends. Of particular importance is returning a more natural role to fire. In the Blue Mountains, for example, Forest Service resource managers are prescribe burning about 1800-2400 ha per

year, but they realize that 10 times this area requires fire treatment annually to achieve management objectives (Mutch 1992).

Inland Maritime Province

The Inland Maritime Province (IMP) spans northeastern Washington, northern Idaho and northwestern Montana (figure 5). This NRM subregion includes the Selkirk Mountains of northern Idaho, plus adjacent parts of Washington, the northern Bitterroot Range, and Cabinet Mountains, the Whitefish Range, the northern Swan Range and the west slope of the Continental Divide in Glacier National Park. As the province's name implies, IMP is relatively moist. Pacific coastal air masses follow well-defined storm tracks which bring abundant moisture to all elevations. The lowest valleys receive more than 50 cm annually, although some localized rainshadows may record 40 cm or less. Warm, dry weather usually prevails during July and August.

Occurrences of breeding great gray owls are recorded by Bergeron *et al.* (1992) for the Montana portion of IMP. Sighting reports on file at the Forest Service's Northern Region Office place the great gray owl in mature western larch, Douglas-fir and lodgepole pine forest communities within the Swan Valley and the Coram Experimental Forest located on the Flathead N. F. Great gray owl breeding in these localities is only suspected. Large expanses of the Swan Valley consist of a mosaic of old-growth forest, wet marshes and grassy meadows, as well as extensive logged-over units, while the Coram Experimental Forest is contiguous to clear-cut tracts. Great gray owls have also been reported for the Kootenai N.F. (MT), Clearwater N.F. (ID), and Idaho Panhandle N.F. (ID), all of which occur within the maritime climatic province (Idaho Conservation Data Center, Boise, ID). These have included sightings of one adult and one young great gray owl in a riparian western red-cedar forest along the Upper Priest River, Bonner County, ID.

Major Forest Service forest types present in IMP include Type #21, ponderosa pine; Type #22 western white pine; Type #25 western larch; and Type #26, lodgepole pine (1977). Kuchler (1964) potential natural vegetation types include: K-11, ponderosa pine, K-12, Douglas-fir, K-13, cedar-hemlock-pine, K-15, spruce-fir. Within those parts of the IMP supporting western white pine forests, a major biotic influence for the past century has been white pine blister rust (*Cronartium ribicola*). Although western white pine is a fire-dependent seral species, the mortality caused by blister rust no doubt altered natural fire cycles and average fire intensities

throughout IMP's montane zones.

Reduced summer moisture in IMP sets the stage for wildfire. Historic fires are believed to have perpetuated certain xeric vegetation types in climatically moist parts of IMP. Typically, the forest zones contain combinations of the following dominants, ranked from highest to lowest drought resistance (Minore 1979): ponderosa pine, lodgepole pine, Douglas-fir, Engelmann spruce, grand fir, western larch, subalpine fir, western-red cedar, pacific-yew (*Taxus brevifolia*), western white pine, western hemlock, and mountain hemlock (*Tsuga mertensiana*).

Precipitation increases with elevation, often reaching and exceeding 200 cm annually; a large portion (75-85%) of this annual moisture falls as snow between September and March. Spruce-fir forests are developed on the higher IMP mountain slopes, while white-bark pine is locally abundant on warm aspects that experience some mid-summer moisture shortages. Although mountain hemlock joins subalpine fir, forming closed-canopy forests on the Montana-Idaho state line, this hemlock is very intolerant of summer drought and heat as well as severe continental winters (Habeck 1987). Upper timberline develops at 2000-2300 m and features krummholtz subalpine fir, white-bark pine, and partly wind-shaped alpine larch (*Larix lyallii*). White-bark pine, a five-needled pine like western white pine and limber pine, has shown significant recent reductions in its abundance throughout NRM due to white pine blister rust epidemics of mountain pine beetle (*Dendroctonus ponderosae*) (Arno and Hoff 1989, Hoff 1992, Keane and Arno 1993).

Fires occur at much lower frequencies (100-200 yr intervals) in this moist geographic subregion. When fires do occur, however, they are often high-intensity, stand replacing fires. The high intensity is due to greater organic fuel accumulations. When the right combination of midsummer weather occurs (lightning, low humidity, wind, dry ground fuels, etc), IMP forests experience wildfires capable of removing all aboveground plant cover (Habeck and Mutch 1973). Western larch, lodgepole pine and/or western white pine are important post-fire seral species which form dense, even-aged pioneer stands. Examples of short-interval "double" or "triple" burns have historically occurred in parts of IMP, and forest recovery may be retarded for many decades.

The deep snow accumulations in IMP mountains cause frequent snow avalanches. Tons of flowing snow and fierce winds smash and mangle the vegetation in the snow track. Snow slide chutes often support vegetation dominated by such woody dicots as mountain alder (*Alnus sinuata*), service-berry

(*Amelanchier alnifolia*), mountain maple (*Acer glabrum*), black cottonwood (*Populus trichocarpa*) and quaking aspen.

Historical Changes in Rocky Mountain Vegetation

Over the past century, the Northern Rocky Mountain forest cover that has served as forest owl habitat has undergone significant change in structure and composition. Popular news media have reported on the diminishing conifer timber volume available for harvest throughout the Rocky Mountains, focusing especially on the current scarcity of old-growth forests, lost after a century of logging.

The descriptions and discussions of each Rocky Mountain phytogeographic province included brief assessment of the ecological roles of climate, fire, logging, and grazing in terms of their impact on early-day and present-day cover. A review of pertinent forest ecology literature for western North America clearly identifies several anthropogenic influences as critical in altering forest and grassland landscape patterns. Native American burning significantly supplemented natural lightning ignitions in establishing fire regimes that altered forest cover types over much of the northern Rockies. Throughout much of the NRM, the lodgepole pine cover type was perpetuated by pre-1900 fires. Lodgepole pine communities occupy a wide range of elevations, and in association with clearcuts or mountain meadows, are often identified as important great gray owl habitat throughout the Rockies. Historic, high-intensity, stand-replacing fires in many cases created even-aged stands but also generated landscapes that prominently displayed a heterogeneous mosaic of lodgepole pine communities of multiple ages (Clements 1910, Lotan *et al.* 1985).

In some parts of its Rocky Mountain range, lodgepole pine appears to function as a climax species, forming communities with several age classes. In the GYA (parts of Idaho, Wyoming, and Montana), fire-free intervals in some lodgepole pine stands historically spanned several centuries (Romme 1980, 1982). Further north, in western Montana and the Glacier Park Ecosystem, lodgepole pine forests were originally subject to stand-replacing fires at intervals of 50-100 years. Brown (1975) provided a graphic interpretation (figure 10) of the complexity of interactions between lodgepole pine community dynamics and fire cycles. In close physical association with many lodgepole pine-dominated stands were groves of fire-dependent quaking aspen that form distinct communities.

Ponderosa pine, a widely distributed forest species in the Northern Rockies, occupies warm, dry lower timberline forest zones that in pre-settlement times frequently burned. These fires perpetuated ponderosa pine savanna/grassland communities with old-growth forest structure. When observed by Leiberg (1899), portions of western Montana mountain ranges displayed a fire-generated ponderosa pine-dominated zone extending from valley bottom to the spruce-fir zone spanning the entire Douglas-fir zone. Such observations suggest that frequent fires maintained potential mesic Douglas-fir types as pine savanna and bunchgrass communities (Habeck 1990). In the more moist mountains of northern Idaho, northeastern Oregon and northwestern Montana, western larch and western white pine serve as major post-fire seral dominants. Western larch and western white pine are relatively long-lived with fire intervals of a century or longer. These two species formed expansive old-growth forests that became the targets of early logging activity (Hutchinson and Winters 1942).

Beginning in the late 1800s, logging removed large expanses of the most accessible montane-zone timber throughout the area designated as the Northern Rockies. The demand for railroad ties, mine timbers, home construction, fuel, and

other uses associated with frontier development during the 1870-1900 period, led to the extensive removal of timber cover and disruption to the original landscape mosaic. Mineral prospecting in western Montana and northern Idaho sometimes involved wholesale burning of the forest simply to expose bedrock. Clearing lands by logging and burning was also done by pioneer farmers, ranchers, and other homesteaders. Sheep and cattle grazing enterprises started by using natural mountain grasslands and alpine meadows; such grazing soon expanded into logged and burned timberlands throughout the middle and northern NRM. Logged and heavily grazed lands were invaded by exotic plants (Losensky 1987, Tyser and Key 1988, Rice *et al.* 1992). The exotic plant species further altered the structures and compositions of native grasslands, meadows, range lands, and even clearcut forest habitats, all of which, in their original condition supported rodent populations used by forest owls.

An analysis of USDA Forest Service timber inventory data dating back to the 1930s (Losensky 1993) provides an opportunity to make a tentative comparison of early-day vegetation cover values with similar modern data compiled from LANDSAT photo interpretations (NDVI map = Normalized Difference Vegetation Index map; Hann *et al.* 1993).

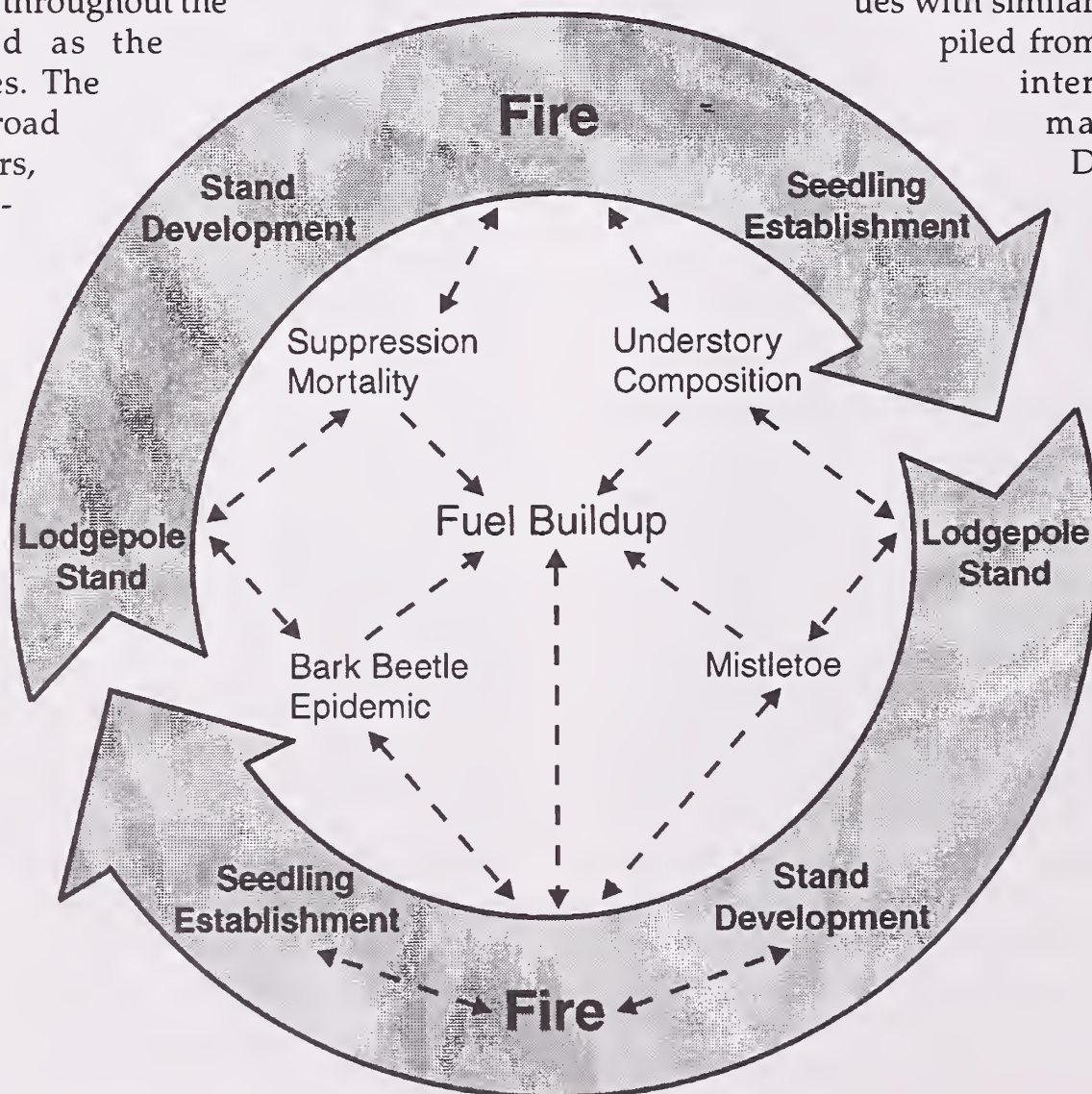


Figure 10.--Typical *Pinus contorta* fire cycle showing interactions between fire and various biotic influences in the northern Rocky Mountains. After Brown (1975).

This comparison allows a coarse scale assessment of historical changes over a 72.5 million ha portion of the Rocky Mountains (USDA Forest Service, Northern Region National Forests and contiguous lands of all ownerships). Table 3 demonstrates that some forest types have been greatly reduced in acreage over the past six decades, though some have increased. This tabulation, however, does not reveal the fact that many of the earlier acres supported old growth. Ponderosa pine savanna, western white pine, and grasslands have been reduced significantly throughout the northern Rocky Mountain region, while sagebrush and agricultural cropland cover types have expanded. Furthermore, alterations in native vegetation and natural ecosystem processes (fire and succession) in the Rocky Mountains have contributed to insect, fungi and disease impacts on the ecosystems of this region (Monnig and Byler 1992, Mutch *et al.* 1993).

OREGON CASCADES AND CALIFORNIA SIERRA NEVADA MOUNTAINS

Introduction

Range maps published by Johnsgard (1988) and Forsman and Bull (1989) describe the great gray owl's range as including the Cascades in Washington and Oregon, southward into the Sierra Nevada Mountains of central California. Specific studies by Goggans and Platt (1992) place breeding populations of *Strix nebulosa* in the central-western Oregon Cascades (Willamette National Forest). Similar studies in the south-central Cascade Range owl studies have been reported by Forsman and Bryan (1984), Bryan and Wise (1985), Bryan and Forsman (1987), and Wise and Lightly (1988), all of which have been centered east of Crater Lake National Park. The volcanic Cascade Range in southern Oregon becomes interrupted by the Klamath River Valley near the Oregon-California border. North of this gap in the Cascades, the mountains are covered with dense montane and subalpine forests adapted to moist conditions (Arno and Hammerly 1984). Southward from the Klamath River, the Cascades display more open-canopied montane forests, adapted to a drier climate. Within northern and northeastern California, the Cascades merge into the granitic Sierra Nevada Range. Our understanding of great gray owls in central California's mixed conifer forests is mostly the result of studies conducted by Winter (1986). He discovered that great gray owl concentrations were greatest in the Yosemite Ecosystem, which includes Yosemite National Park plus the adjoining

Stanislaus, Inyo, and Sierra National Forests.

All along the crest of the northern and southern Cascades, numerous volcanic peaks and cones rise above the forested mountain slopes. Timberlines and alpine habitats are present at the highest elevations along the crest (3700-4200 m). The north Cascades exhibit a distinct maritime climate with precipitation reaching or exceeding 250 cm annually. Southward the maritime influence diminishes with dry summers (July-August) common in the southern Cascade Range, although winter snow depths are still considerable (13 meters on some mountain peaks). Throughout the Cascade and Sierra Nevada mountain range systems, the eastern slopes lie within a conspicuous rain shadow zone. Thus, while the west slopes display dense stands of Douglas-fir and western hemlock supported by the constant supply of moisture, the dry, warm, sunny east slopes support savanna communities dominated by ponderosa pine.

Subalpine fir, according to Arno and Hammerly (1984), becomes less common at timberline in the southern Cascades, and very scarce in northern California. Perhaps it is less capable of withstanding the dry summer conditions prevailing in the Sierra Nevada. In southern Oregon pacific silver fir (*Abies amabilis*) is replaced by California red fir (*Abies magnifica*). In California red fir may reach upper timberline but is less common than mountain hemlock or white-bark pine at the highest elevations. Dry summers and soils derived from volcanic rocks (including pumice) in the southern Cascades create circumstances where moist mountain meadows become less common. The dry soils with reduced fertility support only sparse vegetation in pumice flats ecosystems (Franklin and Dryness 1973, Arno and Hammerly 1984, Volland 1985).

Fire has been a major influence throughout Pacific Northwest (PNW) forests, shaping the landscape's vegetative cover for thousands of years (Agee 1990, Walstad *et al.* 1990). Modern fire suppression has reduced the acreage burned by free-ranging wildfires, which has changed in the forest mosaic, creating more uniform landscapes and higher fuel loadings all across the Cascade Mountains. The ponderosa pine forests in the Cascades historically experienced frequent, low-intensity fires that formed a mosaic of different-aged patches. Fire exclusion has led to major disruptions in ponderosa pine communities, creating stagnated, two-story stands with ladder fuels that threaten the surviving, remnant old-growth pines (Agee 1990).

The Sierra Nevada is a fault-block granitic mountain range that extends over 600 km north-to-south

from the Oregon Cascades. The Sierra Nevada crest (over 3050 m) is off-centered to the east, with the west slope a gradual incline (Arno and Hammerly 1984, Barbour 1988). The west slope receives ample, dependable moisture from the Pacific, except during the dry summer months. Yosemite National Park's montane forest zone receives 100-125 cm annual precipitation. Timberline and alpine zones receive even more, mostly as snowfall. Great gray owl habitat in the Sierra Nevada consists of mixed-conifer forests found between 1200 and 2450 m (Verner 1980, Winter 1982, 1986). Meadows and forests with abundant large snags appear to be important.

The forest vegetation known to be associated with the great gray owl in Oregon's Cascade Range and California's Cascade/Sierra-Nevada Mountains will be discussed below. The conservation assessment prepared for the California spotted owl (Verner *et al.* 1992) includes detailed reviews of the history of California's central Sierra-Nevada mixed-conifer forest types, and should be consulted.

Central-Western And Southcentral Oregon Cascades

Central-Western Cascade Range

The central-western Cascade Range, which includes the Willamette National Forest east of Eugene, Oregon, occupies the central portion of the Western Cascade physiographic province as described by Franklin and Dryness (1973) occupying the montane forest zone between the Willamette Valley and the High Cascades. It is in this geographic area that Goggans and Platt (1992) made their breeding-season observations of great gray owls. Also, it coincides with the mountain landscape (vicinity of the H.J. Andrews Experimental Forest) where Morrison and Swanson (1990) provided a detailed analysis of fire history and vegetation patterns. The lower west slopes (300-1050 m) fall within Kuchler's (1964) potential vegetation Type K-2, western red-cedar/western hemlock/Douglas-fir, while the mid-to upper west slopes (1050-1550 m), are included in Type K-3 where Pacific silver fir-Douglas-fir prevail. Kuchler's Type K-4, subalpine fir-mountain hemlock occupies the Cascade Crest.

Within Type K-2 ("western hemlock zone"), the principal seral species is Douglas-fir, with western white pine, incense-cedar (*Libocedrus decurrens*) and sugar pine (*Pinus lambertiana*) present as occasional seral species (Franklin and Dryness 1973, Morrison and Swanson 1990). Western red-cedar, a tolerant climax species, codominates with western hemlock. Western red-cedar may initially appear with Dou-

glas-fir immediately after fire disturbance or invade gradually over a century following a burn. In Type K-3 ("Pacific silver fir zone"), Pacific silver fir is the climax dominant, with western hemlock and western red-cedar joining as minor climax associates. After logging or fire disturbance in the silver fir zone, Douglas-fir and/or noble fir (*Abies procera*) are the most common seral species. Western white pine is a minor seral species within this higher west slope forest zone.

Forest cover in the west-central Cascade Range is essentially continuous with occasional interruptions by talus slides, rock outcrops, snow avalanche tracks, some dry and wet meadows, and bogs. Actually, according to Goggans and Platt (1992), few natural openings existed previous to modern logging. Morrison and Swanson (1990) determined that their study areas experienced natural fire intervals from 95 years (lower elevations) to 149 years (cooler, moist sites); the latter sites generally experienced stand-replacing burns, the former sites, fires of lower severity. Between 1800 and 1900 fires created a complex mosaic of stands or forest patches, mostly less than 10 ha in size. Fire suppression has operated effectively since 1900.

Great gray owl roosting and nesting habitat in the west-central Cascades features remnant old-growth Douglas-fir. Owl nests were reported by Goggans and Platt (1992) in broken topped, dead Douglas-fir trees, 90-128 cm dbh, all on west-facing slopes. Natural meadow communities are uncommon in the owl sighting areas. Logging activity, however, had occurred within 200 m of all nests. These investigators believe that timber harvesting created "temporary meadows" with hunting perches (tree stumps and snags) suitable for the great gray owls (Miller 1991).

Southcentral Cascade Range

The southcentral Cascade Range (figure 11) falls primarily within Franklin and Dryness's (1973) Basin and Range physiographic province. The area is characterized by fault-block mountains enclosing basins with internal drainage. Bryan and Forsman (1987), reporting on the biogeography and ecology of great gray owls in this segment of the Oregon Cascades, specifically identified Deschutes, Klamath, Lake, and Jackson Counties as the localities of greatest great gray owl abundance.

Much of the forested portion of the eastern flanks of the Cascade Range in Washington and Oregon, including the south-central Cascades, falls within Kuchler's (1964) Type K-10, Ponderosa Shrub Forest (ponderosa pine, *Ceanothus velutinus*, *Cercocarpus ledifolius*, *Purshia tridentata*, *Agropyron spicatum* and

Festuca idahoensis). This same forested region is classified as the ponderosa pine zone by Franklin and Dryness (1973), and in Oregon the pumice plateau area occupies elevations between 1450 to 2000 m. At its upper limits the ponderosa pine zone grades into forests dominated by Douglas-fir, grand fir, or *Abies concolor*. At its lower limits the pine zone abuts *Artemisia tridentata* steppe or western juniper (*Juniperus occidentalis*).

Franklin and Dryness's (1973) literature review of the ponderosa pine zone in Oregon emphasizes the major role that historic fires played in shaping the vegetation mosaic in south-central Oregon. They report on fire history studies, such as those made by Weaver (1943), that indicate fire occurrences at 8-20 yr intervals in the ponderosa pine zone. Frequent fires maintained ponderosa pine dominance even on mesic habitats where the potential climax species, such as Douglas-fir, would attain dominance without frequent fire treatments. Fire exclusion over the past half century has allowed the development of dense, stagnated ponderosa pine stands, or invasion of shade tolerant climax species. Fire suppression combined with heavy livestock grazing has altered understory vegetation, too. Heavy grazing often favors increased shrub cover and reduced grass cover (Franklin and Dryness 1973). Logging in the ponderosa pine forests has accelerated the conversion to shade-tolerant species such as Douglas-fir and grand fir.

The forest types primarily used by great gray owls in south central Oregon are dominated by mixtures of mature and/or old-growth lodgepole pine and ponderosa pine forest (Bryan and Forsman 1987), especially stands adjacent to wet meadows. Quaking aspen is associated with lodgepole pine on mesic-moist sites in their owl study areas.

California Sierra Nevada Range

The southern Oregon Cascades merge physically and phytogeographically with the Sierra Nevada Range in California. A pronounced moisture-temperature gradient means the cool, moist environments of western Washington and northwestern Oregon give way southward to warmer, drier climates. Southern Oregon displays an increase in the number of California-centered floristic elements, such as sugar pine, incense cedar and tanoak (*Lithocarpus densiflorus*). These elements, along with others typical of the mixed conifer and mixed sclerophyll forests, are parts of the transition to typical northern California vegetation types (Franklin and Dryness 1973).

Arno and Hammerly (1984), include the mountain-

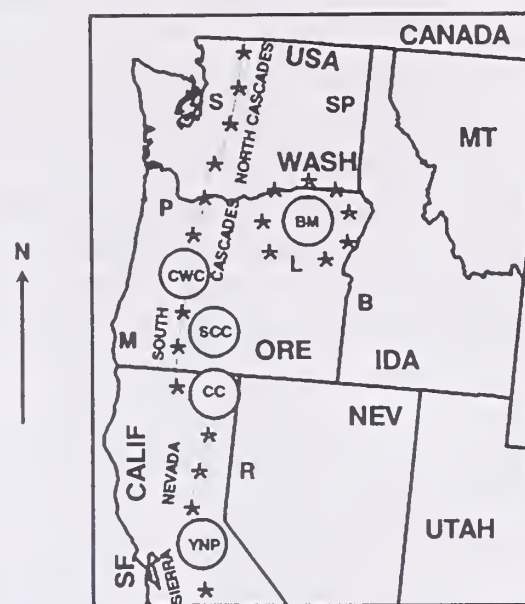


Figure 11.--Cascade and Sierra Nevada mountain ranges and general localities where great gray owl studies have been reported. BM = Blue Mountains, CWC = Central Western Cascades, SCC = South-Central Cascades, CC = California Cascades, and YNP = Yosemite National Park. Other geographic points: B = Boise, ID; SP = Spokane, WA; S = Seattle, WA; P = Portland, OR; L = La Grande, OR; M = Metford, OR; R = Reno, NV; SF = San Francisco, CA.

ous northeastern portions of California, southward to Lassen Peak (the region north of the Feather River), within their "Southern Cascade Range" designation. The similarities are so great between northeastern California's forest vegetation (Klamath N. F.) and that which occurs in Oregon's south-central Cascades that Miller (1991) undertook a detailed habitat analysis to assess the great gray owl's status in the northern California extension of the Cascade Range but he found no owls occupying his California study site.

The California Sierra Nevada (figure 11) forest vegetation is treated (literature review) in detail by Arno and Hammerly (1984), and Barbour (1988). Within the USDA Forest Service's California spotted owl conservation assessment (Verner *et al.* 1992), McKelvey and Johnson (1992) and Weatherspoon *et al.* (1992) discussed forest vegetation and fire ecology of the central Sierra Nevada. Their reports cover the historical impacts of early logging and pre-settlement fire regimes.

Barbour (1988) provided a gradient analysis diagram (figure 12, redrawn from Vankat, 1982) of Sierra Nevada vegetation types. This ordination encompasses the central Sierra Nevada forest vegetation types used by great gray owls and was studied in detail by Winter (1982, 1986). The major forest types, as classified in the 1977 USDA Forest Service treatment include Type #21, Ponderosa Pine; Type #23, Fir-Spruce; and Type #26, Lodgepole Pine. All

of the Sierra Nevada, under consideration here, falls within Bailey's (1978) Ecoregion M2610, "Sierran Forest Province."

The forests of the Sierra Nevada between 600 and 2000 m mostly fall within Kuchler's (1964) Type K-5, "Mixed Conifer Forest," in which white fir (*Abies concolor*), incense cedar, ponderosa pine and Douglas-fir codominate. On a revised Kuchler map of California's natural vegetation, dated 1977, this same category is designated as Type K-15, "Sierra Montane Forest," positioned above Type K-7, "Sierra Yellow Pine Forest" which features ponderosa pine. Present, at higher elevations (1800-2750 m), is Kuchler (1964) Type K-7, "Red Fir Forest," featuring California red fir as a primary dominant, with white fir, lodgepole pine, Jeffrey pine (*Pinus jeffreyi*), and western white pine as common associates. On Kuchler's 1977 revised vegetation map, this latter zone is redefined and described as K-17, "Upper Montane-Subalpine Forest."

Winter (1986) identified the Sierra Nevada elevational range occupied by breeding great gray owl populations to be between 1219 and 2438 m. Foraging sightings were nearly always in or near montane meadows, and nests in the tops of broken-off large snags. Winter (1986) estimated that old-growth red fir/mixed conifer forests in the central Sierra Nevada national forests and national parks have been reduced from nearly 2,000,000 ha down to about 400,000 ha, an 80% reduction; he also suggested that earlier logging on national forests led to significant reduction in large-diameter snags available as owl nest sites.

Within the central Sierra Nevada mixed conifer forest type, Barbour (1988) identifies ponderosa pine as "the thread that holds the type together," although on drier and colder sites, Jeffrey pine may replace ponderosa pine. Prior to modern fire suppression, the pine-dominated mixed conifer forests had an open, park-like appearance with groups of large-diameter, taller pines alternating with openings, with few trees of intermediate height present. Overstory and understory structure in the mid-montane mixed conifer forests changed during the past century in response to fire suppression.

Prior to 1875, fires occurred in the Sierra Nevada mixed conifer zone at intervals of about 8 years on pine-dominated sites and about 16-year intervals on the more mesic fir-dominated sites (Barbour 1988). Most early-day fires, of Indian or lightning origin, were low-intensity ground fires and of limited areal extent. Frequent fire created conditions for successful conifer seedling establishment. The periodic burning routinely thinned out conifer reproduction,

maintaining the open-canopied park-like conditions. After 1900, when fire suppression became successful, the original, open pine-dominated forests experienced invasions by white fir. The forests now have higher amounts of dead and living fuels, which enhance the potential for crown fires in the Sierra Nevada mixed conifer communities (Weatherspoon *et al.* 1992). Opportunities for ponderosa pine establishment have also been reduced considerably.

The California red fir forests type, occupying the upper montane zone of the Sierra Nevada, often features lodgepole pine as a common associate; lodgepole pine also extends upward into the subalpine forest zone. Barbour (1988) describes the presence and dominance of red fir on mesic habitats where lodgepole pine is only a minor component. Where lodgepole pine is prevalent, it forms stands that are moderately dense, with 55-80% cover. Barbour (1988) states that lodgepole pine in the Sierra Nevada does not form a fire-type as it does in the Rocky Mountains.

Both red fir and lodgepole pine form old-growth stands; but the fir achieves ages over 300 years and diameters over 100 cm dbh, while lodgepole lives less than 300 years and measures under 70 cm dbh. Studies of lodgepole pine in California have shown

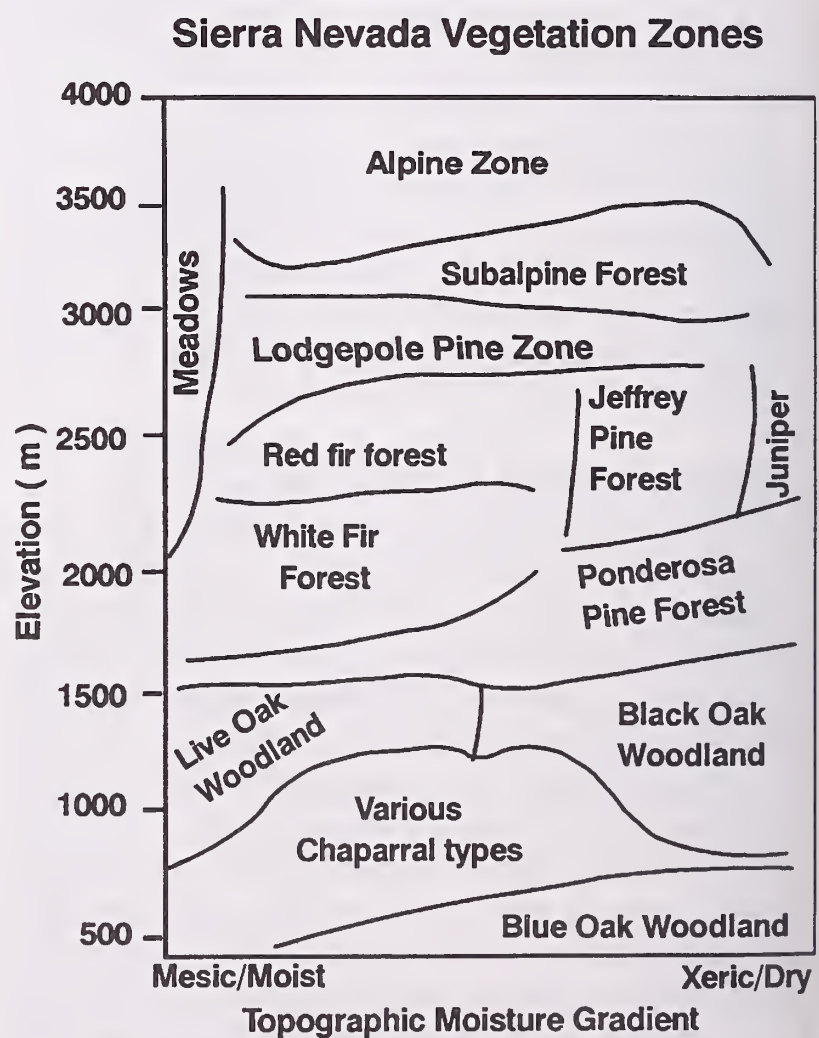


Figure 12.--Ordination diagram representing general arrangement of major vegetation zones along elevation and topographic-moisture gradients in the Sierra Nevada Range, California. After Barbour (1988) and Vankat (1982).

it to be bimodal in its site distribution pattern, capable of occupying both arid, wind-swept, shallow soils and successfully invading wet meadow edge and lake shore sites in cold-air drainages (Barbour 1988). On such wet sites lodgepole pine and red fir may also be co-associates, with quaking aspen and black cottonwood also present. Barbour (1988) cites studies by Vankat and Major (1978) suggesting that lodgepole pine invasion of wet meadows may be related to fire cycles. Other biologists have implicated episodic insect infections in lodgepole pine population dynamics in the upper montane Sierra Nevada zone.

The forest dynamics, involving several pairs of tree species, within the ecotone between the mid-montane and the upper montane is discussed by Barbour (1988). Basically, white fir gives way to California red fir, ponderosa pine to Jeffrey pine, and sugar pine to western white pine. Mixed through these conifer forest types may be quaking aspen stands, occupying an elevational range between 1500 and 3000 m. According to Winter (1986) mesic-moist meadows are well represented in the Sierra Nevada below 1200 m elevation, but he found no evidence that such sites were used for breeding by great gray owls. He suggested that summer heat at lower elevations might be stressful to great gray owls, which evolved in boreal holarctic climates.

Historical Changes in Cascade and Sierra Nevada Vegetation

As with Rocky Mountain vegetation, the lower and upper forest zones in the Cascade Range and Sierra Nevada have experienced a century of major disturbance by elements of western civilization. Mining, logging, grazing, and altered fire regimes have all combined to change vegetation patterns in the lower and upper montane zones where great gray owls historically occurred (Forsman and Bull 1989, Verner *et al.* 1992, Winter 1986). Systematic field investigations in the Oregon and California mountains were initiated before 1900. The U.S. Geologic Survey (USGS) prepared reports on the condition of natural resources within federally established forest reserves, areas which later became the national forest system. McKelvey and Johnson (1992) have summarized USGS data on pre-1900 tree species distributions, timber volumes, and logging intensities in what now constitutes Yosemite National Park and adjacent national forests.

McKelvey and Johnson (1992) cite circa 1900 data compiled by USGS's forest examiners George Sudworth (1900) and John Leiberg (1902), wherein

the claim is made that about 0.6 million ha had been logged in the northern Sierra Nevada between 1850 and early 1900s, leaving about 0.9 million hectares uncut at the beginning of this century. The timber volume removed per stand, however, was highly variable, ranging from an estimated 5% to 99% but averaging about 50% for all areas examined by the early USGS field observers. Log transport limitations, namely horse-drawn wagons, prevented clearcutting in many instances and necessitated "light high grading" of old-growth ponderosa pine and sugar pine. Thus, some Sierra Nevada old growth survived by simply being out of easy reach. Wherever railroad transportation was available, logging was more intense. The volume of timber removed from Sierra Nevada national forests rose steadily between 1900 and 1960, then declined somewhat and leveled-off until the 1980's when it rapidly declined. Rates of timber harvest rose again during the early 1990s (McKelvey and Johnson 1992).

McKelvey and Johnson (1992) concluded that the Sierra Nevada Range currently supports very little pristine forest cover. They state that logging, grazing and altered fire regimes have converted the pre-1900 forest system dominated by large, old, widely spaced trees, and with high structural heterogeneity, into a system characterized by densely stocked, even-aged stands in which most of the largest trees are in the 80-100 yr class. The modern Sierra Nevada forest appears, to these two investigators, unstable, to be highly susceptible to drought-induced mortality and threatened by insect infestations. In their current condition, many Sierra Nevada forests display very high fire potential, a subject which is thoroughly discussed by Weatherspoon *et al.* (1992).

Summary: Relationships Between Forest Dynamics and Management of Great Gray Owls

In summarizing what we know about the character of forest and meadow types used by the great gray owl in western U.S., a two-part theme repeats itself: great gray owls use old-growth forests near openings. The old-growth forests provide large-diameter (over 50 cm dbh) trees or snags having abandoned raptor nests, and the openings provide huntable populations of rodents. During the past century, human activities, including widespread harvesting of mature and old-growth forests, have reduced the abundance of potential nest trees. Furthermore, the altering of natural (pre-settlement) fire regimes have disrupted the generation and maintenance of a distinctive fire mosaic covering the west-

ern North American landscape.

Timber harvesting, whether clearcuts or even selective removal of large-diameter trees, has reduced nesting opportunities for all forest raptors, including great gray owls. Studies show that logging can and does generate "temporary meadows" capable of supporting rodent populations used by breeding great gray owls. But unlike naturally occurring mountain meadows, forest clearings created by logging undergo rapid forest re-establishment; successional development makes the usefulness of such openings short-lived. Some montane grasslands have experienced gradual conifer invasions, attributable to reduced fire occurrence and fostered by shifting climatic cycles. This means shrinking great gray owl foraging habitat throughout western North America. Sustaining populations of great gray owls is possible, but only as a product of innovative ecosystem forest management.

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Conservation Status of Great Gray Owls in the United States

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INTRODUCTION

Previous chapters outlined the biology and ecology of great gray owls as well as the ecology of this species in the western United States. That technical review provides the basis to assess the current conservation status of great gray owls in the United States. Are populations of great gray owls in the United States currently threatened? Are current land management practices likely to lead toward the peril of these populations?

In this chapter I will synthesize the information and conclude that: 1) populations of great gray owls in the United States are secure and will likely remain so given current land management practices; 2) populations of great gray owls are in peril (declining or experiencing some demographic trauma) or are likely to be in peril in the future given current land management practices, or 3) there is insufficient evidence to determine the species' conservation status. A minimum of references are presented here because the literature was reviewed in the previous chapters.

Is the Distribution and Abundance of the Great Gray Owl Declining in All or Part of Its Range?

Great gray owls occupy a vast area in western and north-central United States. The distribution and the abundance of local populations do not appear to have declined systematically in the United States, but few data are available to examine the trend.

Distribution

Available evidence does not indicate any consistent trend, either expansion or decline, in the distribution of great gray owls in the United States. Sites near the great gray's southern range boundary have been continuously occupied for at least several decades. The distribution of this owl has not been thoroughly documented nor is it monitored. Therefore, based on limited knowledge, I conclude that its distribution has not recently changed.

Abundance

Except in a few isolated areas, local and regional trends in great gray owl abundance cannot be assessed with available data. Most documented breeding populations of great gray owls have not been monitored more than 2-3 years, a period too short to discern a long-term trend in a species that preys upon fluctuating populations of vertebrates. In Oregon, Bull *et al.* (1989) documented stable reproductive success over a 4-year period (she currently has 10 years of data with only one poor reproductive year—E. L. Bull pers. comm.). Groves and Zehntner (1990) surveyed for great gray owls during 1989 in the area of Idaho and Wyoming studied by Franklin (1988) from 1980-1982. The 1989 surveys located numerous calling great gray owls but few previously occupied sites were occupied. The 1989 surveys did not provide quantitative evidence for a decline in great gray owls for this area although the authors suggest that a reduction in nests reported by USDA Forest Service crews and birders in the area may suggest a decline.

Do Habitats Vary in Their Capacity to Support Great Gray Owl Populations or to Support Particular Activities of the Owl? What Are the Important Characteristics of Those Habitats?

Studies of habitat use by great gray owls in the western United States and in Canada provide convincing evidence that great gray owls use particular habitats for nesting and foraging. Experimental studies or properly designed mensurative investigations have not been conducted to determine how the pattern of habitat use translates into differences in fitness for owls using various habitats. Despite the lack of data on differences in reproduction and mortality across habitats, existing knowledge based on the observations of habitat use provides sufficient evidence to infer that certain habitats are more valuable to the species than others.

Great gray owls consistently nest in forested habitat. In the western United States, nests occur most

often in mature and older forest stands. An experiment in Oregon employing nest platforms demonstrated that individuals prefer to nest within forest stands rather than on the edge of clearcuts. Because this owl needs a large platform for nesting, large broken-top snags and trees, trees with large stick nests, or trees with large mistletoe clumps are necessary for nesting. These habitat features occur most commonly in mature and older forest stands. Therefore, conclude that patches of mature and older forest are important for great gray owls. Patches of mature forest used for nesting need not be extensive but must occur frequently throughout the landscape. Each patch of mature forest cannot be expected to provide suitable nesting structures because raptor nests, flat-topped snags, and broken-topped trees are rare elements of many forest stands. Finally, younger forest stands with residual older forest components can provide nesting habitat.

Quality foraging habitat occurs in a variety of vegetation structures but does not include dense, young forest stands. Small meadows, open forest, treed muskeg, and clearcuts with residual perches were reported as important foraging habitat in different studies. During winters when snows crust in meadows and clearcuts, open mature and older forest may be important foraging habitat.

Do Habitats Vary in Their Capacity to Support Principal Prey Species?

Microtus voles and pocket gophers dominate great gray owl diets in populations studied in the western United States and Canada. Populations of *Microtus* are more abundant in grasslands and less common in closed-canopy forests. Pocket gophers inhabit forested and unforested habitats but also are not abundant in closed canopy forest.

Red-backed voles are the only other prey species representing over 10% of the owl's diet in a major study in North America. These voles inhabit forest environments and are most abundant in mature and older forests (see Chapter 9). Studies of great gray owls in Oregon, where red-backed voles are preyed upon, did not establish whether great gray owls captured the voles along forest edges or in the forest interior.

If the Great Gray Owl or Its Prey Relies on Specific Habitats, Are These Habitats Declining or Being Stressed by Current Management?

A long history of fire suppression, livestock grazing, and timber harvest has altered forest structure

of montane forests in the Rocky Mountains. These changes have resulted in both positive and negative consequences for great gray owls. As described in Chapter 15, presettlement fires occurred at shorter intervals resulting in forests with lower canopy cover than observed today. A combination of grazing and fire suppression have contributed to invasion of conifers into meadow and grassland communities in the montane zone. Loss of natural meadows and grasslands, especially small open habitats within forested landscapes, degrades foraging habitat for great gray owls. In some areas this trend continues today. Similarly, increased canopy cover and the resulting decrease in understory reduces habitat quality for potential great gray owl prey and results in forest structure less suitable for great gray owl foraging.

Clearcut and partial cut timber harvests have created new foraging habitat in many areas. The quality of this habitat depends on many factors, particularly the size of the harvest units and the availability of hunting perches. Portions of harvest stands over 30 m from an edge or perch are of little value. Therefore large harvest units without residual forest or snags provide less foraging habitat than an equivalent area of many small units. Timber harvest during the past 3-4 decades has relied largely on clearcutting. Therefore, foraging habitat has increased in many areas. The increase in foraging habitat will be short-lived in some cases, compared to the lifetime of natural meadows. The establishment of dense regeneration on clearcut units renders the site unsuitable for foraging until later in succession when the forest stand opens through tree mortality. In cases where forest does not establish after harvest, the new foraging habitat will be long-lived.

The increase in foraging habitat that often results from clearcutting has in some instances been offset by pocket gopher control practices used in forest regeneration. Pocket gophers are intensively controlled on some forests through poisoning gophers in their burrow systems. Data are not available to evaluate whether great gray owls are indirectly poisoned through these efforts; however, if the practice is successful in reducing pocket gopher populations, foraging habitat quality is reduced.

While clearcuts may provide temporary foraging habitat, timber harvest may remove nesting habitat. In many areas of the Rockies, especially in the Southern Continental Province and to a lesser extent the Northern Continental and Intermountain Provinces, mature and older forest stands represent a minority of the landscape (table 1, Chapter 15). In eastern and central Oregon the remaining old forest is a small

fraction of the original old forest. Existing older forests are generally more valuable and thus selected for harvest. Therefore, even modest reductions of mature and older forest through timber harvest can have a long-term impact on available nesting habitat. These mature and older forests frequently occur in topographic sites that are less likely to burn. Following the removal of these stands, management of alternative stands to provide nesting habitat may be difficult because of the higher probability of fire.

Reductions in mature and older forest habitats must be considered potential reductions in great gray owl nesting habitat. This owl will nest in small patches of mature forest but only if suitable nesting structures exist. Therefore maintenance of nesting habitat depends most on the dispersion (rather than aerial extent) of sites with suitable nesting platforms. Based on historic patterns of timber management, nesting habitat is being stressed and has been degraded through past forest management.

Do the Life History and Ecology of the Great Gray Owl Suggest That Populations Are Vulnerable to Habitat Change?

Platform Nesting

Great gray owls nest primarily on old raptor nest platforms or broken-topped trees and snags. These structures occur most commonly in mature and older forest stands. Although individual great gray owls do not need a large stand of older forest for nesting, landscapes must have sufficient mature and older forest to produce a sustained "population" of well dispersed suitable nest structures. Therefore, the aerial extent of mature and older forest necessary to support a great gray owl population must be greater than the extent of stands with nesting great gray owls in any given year. The dynamics (production and survival) of nest platforms (including raptor nests, broken-top snags, etc.) are unknown so estimating the area of forest necessary to sustain sufficient nesting sites is not possible given current knowledge. This aspect of great gray owl ecology indicates that the species is vulnerable to habitat change. Because the species does not require large nest stands, management of nesting habitat should not be difficult, once the dynamics of nest platform populations is understood.

Productivity and Survival

Populations of great gray owls studied in North America exhibit relatively high, constant productivity for a large bird. Clutch size, nest success, and age of first reproduction each appear strong compared to other large owls.

Although a number of investigators have documented productivity of great gray owl populations in North America, few studies report survival and the information available is not precise. Existing estimates indicate relatively high juvenile and adult survival. None of the estimates, however, cover a long time period or examine survival under different environmental conditions. In general, though, existing information suggests that productivity and survival of studied populations are favorable for persistence. Studies in California are an exception, but the methods and rigor of these studies are questionable.

Home Range Size

A limited number of investigations indicate that individual great gray owls use large areas of forest landscapes. Because these owls do not defend their entire home range, densities of great gray owls are higher than their large home ranges would suggest. Despite the potential for several pairs of owls to occur within the area of a single home range, land management must provide habitat with an interspersed nesting and foraging habitat over large areas to ensure population persistence. This aspect of the species ecology indicates vulnerability to decreases in habitat quality at the landscape scale.

Trophic Position

Great gray owls prey upon small mammals, particularly voles and pocket gophers in the western U. S.. As such, they rely on the integrity of 2-3 trophic levels. The probability for persistence of species at higher trophic levels is thought to be less than for primary producers or primary consumers indicating this species is relatively vulnerable to habitat changes which negatively influence lower trophic levels.

What Is the Current and Projected Conservation Status of the Great Gray Owl?

Direct scientific knowledge is insufficient to make a sound judgment of the current conservation status of great gray owls. The species has, however, been investigated in several locales and over a longer period than many owls. These studies provide the basis from which to draw informed but tentative conclusions. Available evidence, although limited and indirect, suggests that the status of the great gray owl varies across its geographic distribution in the United States. Over the short term, persistence of great gray owls appears secure in the Northern

Rockies. Researchers most aware of the owl's ecology in eastern and central Oregon and in California suggest that persistence of the species is less certain in these areas. As a whole great gray owls in the United States occur over a broad geographic range, and evidence from the few populations studied indicates strong reproduction. Furthermore, the life zone occupied by great gray owls is continuous over large areas compared to subalpine and alpine species. Therefore, this owl is not as susceptible to problems associated with small population size as some other species.

Many species of owls are food limited and foraging habitat is critical in maintaining populations (e.g., Korpimäki 1984, Hirons 1985). Great gray owls appear to be similar. Historical forest management has produced positive and negative results for great gray owl foraging habitat. Livestock grazing and fire suppression has created a loss of small natural meadows (used for hunting by the owls) while clearcutting in some cases has created forest openings. The abundance of foraging habitat, then, may be similar to or somewhat greater than in the previous century.

The relationship between nesting habitat structure and nesting success is not understood. Observations of nesting habitat use, however, indicate that great gray owls will nest in a variety of forest conditions given that a suitable platform is present. In Oregon, the abundance of suitable platforms is thought to limit the number of breeding great gray owls (E. L. Bull, pers. comm.). In this area, loss of potential nesting habitat has been severe. Whether this is the case elsewhere is not known; however, management of nest-building raptors will be critical to providing necessary nest sites.

The long-term persistence of great gray owls south of Canada and in Alaska seems likely provided that forests of all successional stages are maintained and well dispersed on a local and regional scale. Persistence on a local geographic scale is less certain. Maintaining persistence will require special attention to the long-term persistence of mature and older forest stands on sites where natural fire is less likely to destroy the old forest and where suitable nesting platforms are abundant. These stands will be necessary to consistently produce nesting structures. Furthermore, mature and older forest likely provide important alternate foraging habitat during periods when crusted snow prevents great gray owls from accessing their preferred rodent prey.

Given the large home ranges used by great gray owls for foraging, management of foraging habitat is critical to maintaining persistent owl populations.

Maintaining quality great gray owl foraging habitat should be compatible with forest management for commodity resources if management takes a long-term view. Natural meadow systems must be maintained and restored through fire management. Similarly, temporal continuity of foraging habitat must be maintained through long-term harvest planning. Harvest units can provide open foraging habitat that is most used by great gray owls. As mentioned above, alternate foraging sites used during critical periods of low prey availability in the primary foraging habitat must also be maintained.

The conclusions reached in this chapter are different from views held by at least one ecologist who has conducted long-term research on great gray owls. The other ecologist feels the short-term persistence of the species is less secure than indicated here and that management of the species will be more difficult than I infer. A summary of the review comments of this ecologist are available upon request.

WHAT ARE THE MANAGEMENT CONSIDERATIONS?

This assessment of the conservation status of great gray owls leads to several consequences for management. Below, I outline several of these.

1. Great gray owls occupy forest landscapes and use habitats from the extremes of the successional spectrum. As a result, management of this species should fit naturally into forest management that provides for commodity development within the framework of conserving biological diversity. This is not to say that haphazard management will accommodate this owl but indicates that, given attention to the owl's habitat, extractive management is compatible with conserving great gray owls.

2. Management of great gray owl habitat must take a long-term view of forest succession and consider landscape and regional forest patterns. Because the owl hunts meadows, treed muskegs, open forest, clearcuts, and other forest openings, disturbance agents such as fire and insects influence foraging habitat quality. Clearcuts are usually short-lived compared to muskeg and meadows; and foraging habitat within clearcut openings will span only 2-4 generations. Even natural meadows are transient under some circumstances without disturbance by fire. Nesting habitat is also succession dependent. Once lost through stand replacement disturbance, nesting platforms will not be replaced naturally for a century or more in many forest types. Similarly, loss of mature and older forest habitats will influ-

ence other raptors (particularly goshawks) that build many of the nest platforms used by great gray owls for nesting.

3. The large home ranges of great gray owls and the resulting dispersed population structure dictate a broad landscape and regional perspective to management. The interacting members of great gray owl populations may inhabit an area greater than individual ranger districts. Interacting subpopulations likely span several National Forests. Therefore, management must be coordinated among administrative units to maintain links between interacting biological units.

4. Efficient, cost-effective progress toward improved management will come most rapidly through cooperative efforts of research and management. This conservation assessment highlights how little is known about the demography, metapopulation structure, and even habitat use of great gray owls. Because the species is not in immediate peril in some portions of its geographic distribution, efforts to obtain further knowledge of great gray owl ecology should be approached with a modest, determined program designed to obtain data efficiently over the long term. This may be accomplished through adaptive management. By examining great gray owl response to alternative management in areas where studies of small mammal dynamics are occurring (in conjunction with other work), management of great gray owls can be improved at low cost.

5. The loss of nesting habitat in central and eastern Oregon has been identified as the most immediate threat to great gray owl persistence in that region. This may be the case in other areas. Therefore, determined management of nesting habitat should be a priority, without which local persistence of the species will be in jeopardy.

6. Within the context of adaptive management, great gray owls represent a classic case upon which to develop ecosystem management. The broad spectrum of habitats used by the owl encompass important ecosystem transitions (among successional stages). The owl consumes vertebrates that are important in forest processes. Finally, the large areal requirements of the owl will force managers to approach planning from a landscape perspective.

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Information Needs: Great Gray Owls

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INTRODUCTION

Current understanding of great gray owl biology and ecology is based on studies of less than five populations. In an ideal world, a strong conservation strategy would require significant new information. However, current knowledge suggests that conservation of this forest owl should involve fewer conflicts than either the boreal or flammulated owl. The mix of forest habitats used by great gray owls fit patterns that occur in managed forest landscapes when the maintenance of mature and older forest is an integral part of management planning. Therefore, immediate threats to the persistence of this owl on a local and regional basis are not great. Long-term threats may be significant if loss of open-structured, mature and older forest continues as in the last century. Addressing the long-term threat to persistence should be the target of management and research planning.

The absence of a current conservation crisis affords the opportunity to examine great gray owl response to forest management over a relatively long time frame and the luxury of building information on the species gradually and inexpensively. A research program could be built around testing potential management guidelines rather than simply gathering the basic information necessary to build the strategy. In this chapter I will assess the strength of existing knowledge in forming a conservation strategy. Then I will discuss efficient strategies for obtaining needed information. This chapter will include few citations because it relies on Chapters 14 and 15 which review literature on this species and some of the forests it inhabits.

STRENGTH OF EXISTING KNOWLEDGE TO FORMULATE A CONSERVATION STRATEGY

Throughout this section I approached each topic as a question. Is our understanding of this topic sufficient to support the development of a sound, na-

tional-scale conservation strategy for the great gray owl? For example, "is the response of great gray owls to stand level habitat change understood in sufficient detail to formulate a conservation strategy?"

Distribution

Systematic surveys for great gray owls have not been conducted in many areas. The owl's large size and its crepuscular activity, however, contribute to detection of individuals. Therefore, the range of great gray owls on a broad scale has been established with reasonable confidence. Delineating local distributions, especially in areas with little human activity, will require specific survey efforts. However, the owl's distribution is understood in sufficient detail to formulate regional conservation strategies.

The nature of links among populations (metapopulation structure) of the species is unknown. This information would aid in defining management units and in identifying habitats that may be critical in joining portions of metapopulations. Molecular studies examining small samples of individuals from populations throughout the species' range could begin to provide this information.

Response of Great Gray Owls to Stand-Level Habitat Changes

Habitat use by great gray owls has not been studied experimentally. Therefore the direct response of great gray owls (e.g., changes in habitat use) to stand-level changes have not been observed. However, observational studies of radio-marked individuals provide sufficient evidence to define broad habitat associations that can be used to develop initial management guidelines.

Knowledge of habitat use should be expanded through short-term, relatively small observational studies in several (four-five) new geographic settings representing forest types not covered in past studies. Understanding of factors influencing habitat use

should be examined through two, more intensive, experimental studies conducted in association with National Forest System commercial forest management. The goal of these studies should be a system to rank habitat quality within a management area for different functional uses (nesting, roosting, foraging).

The relationship between primary prey species and microhabitat should be further examined with the goal of producing predictive models describing the response of prey populations to alternative forest management actions. These studies should not be approached as isolated parts of a great gray owl research program but coordinated with efforts designed to understand the role of small mammals in forest systems and as prey for other forest predators.

Effects of Landscape-Scale Changes on Home Range Use

Studies of great gray owls have not examined the influence of habitat characteristics at the landscape scale on home range characteristics or the reproductive success and survival of individuals and populations. Issues involving habitat use at the landscape scale have not been addressed in any research effort. Existing data show that great gray owls use large home ranges and therefore demonstrate the scale that must be addressed when examining habitat use above the scale of stands.

Effects of Regional-Scale Habitat Changes on Movement Patterns

Studies in Oregon and Canada have shown that great gray owls exhibit a mixed pattern of seasonal and annual movements. In general, adults are sedentary; however, seasonal elevation movements have been documented as well as long distance dispersal of adults and juveniles. Environmental features which influence the survival of dispersing individuals and the paths used during dispersal have not been addressed. Furthermore, how local habitat features influence the probability of individuals dispersing from an established home range is unknown.

Effects of Stand-Level Habitat Changes on Foraging Behavior

Scientific literature on great gray owls includes only general descriptions of foraging behavior. This knowledge is insufficient to begin forming a predictive model of the response of great gray owl forag-

ing success to habitat change. Even the first step of developing a ranking of foraging habitat quality based on habitat structure would be tentative given our understanding of how foraging success changes among habitats. Knowledge of the effects of stand level habitat change on prey populations, prey biomass, and prey availability is crucial to predicting the consequences of forest management. This knowledge is not currently available.

Demography

Although reproduction of great gray owls has been documented in several geographic settings, survival and dispersal are much more poorly understood. In particular, how vital rates vary with habitat conditions is not understood. The interaction between environmental conditions (forest structure, prey populations, predators, competitors, landscape patterns) and demographic parameters must be understood prior to developing comprehensive management plans for great gray owls. This does not mean that management is not possible without data on the demography of every target population. Rather, patterns of change in demography across the species' range should be understood so that a reductionist approach to management is unnecessary.

Dynamics of Primary Plant Communities

Great gray owls inhabit a wide range of forest types. Forests used by this owl coincide with commercially valuable forest throughout much of the species' range. As a consequence, a relatively rich body of scientific literature exists on the dynamics of these forests. Forest ecologists understand the successional dynamics of these forests and the interaction of many of the disturbance agents. Understanding of the dynamics of forest species other than the dominant tree species is less complete. The role of small mammals (major prey of the great gray owl) in these forests is also poorly understood. Ecological processes important in edge habitats such as meadow-forest edges have been studied to some extent but are extremely important to this species and require further study. For example, the ecological interaction between small mammals occurring in meadows (and other forest openings) and forest stands are not well studied.

Broken-topped snags and broken-topped trees are important to great gray owls for nesting. The population dynamic of these structures are not understood and there is no basis from which to predict the stands most likely to produce potential nest structures. Understanding the role of fungi infections

and other pathogens in creation of nest trees will be important in forming the necessary predictive models. A system of ranking various mature and older stands in terms of the probability of providing nesting structures would be useful for management.

History of Distribution and Composition of Forest Communities

Scientists and managers are beginning to focus more attention on landscape history. Managers realize that descriptions of historic environments provide a window, although an opaque view, into the range of variation experienced by organisms in the past. Scientists understand that historical ecology can aid in understanding important ecological concepts such as successional patterns, community theory, and biogeography. Despite increased interest in historical ecology, scientific understanding of the historic abundance and distribution of montane conifer forests in the western United States is not sufficient to indicate how current patterns compare to the past. In particular, knowledge of patterns in distribution and abundance of older age classes of these forests is not available. Describing these patterns is extremely difficult.

Current efforts to put management impacts into a historic context seem to focus almost exclusively on what amounts to a snapshot of vegetation history—a documentation of forest conditions near the time when European settlers first began to impact forest structure. Conservation planning for great gray owls must also consider patterns in these forests thousands of years ago. The value of the historic information lies in the perspective it can provide on the potential variation in great gray owl distribution in the past and the forest conditions the species was exposed to. I do not believe that historical ecology, emphasizing static conditions in recent times, say 100 years ago, will provide the complete picture needed to place present conditions in a proper historic context. Conditions immediately prior to industrial development may have been extraordinary compared to the past 1,000 years or more. Using forest conditions in the 1800's as a baseline, then, could provide a false impression if the baseline is considered a goal to strive toward.

A RESEARCH PLAN

Given the limitations in funds available for ecological research, an applied research plan must consider the urgency of new knowledge and prioritize knowledge to be acquired. A research plan for a species in immediate peril will differ fundamentally

from one targeting a common species. Therefore, a research plan for the great gray owl must be written in light of its conservation status.

Research on the great gray owl is predicated upon several conclusions based on the previous chapters. Scientific understanding of the ecology of great gray owls relevant to conservation is extremely limited. As described above, many important topics have received no attention and existing research is limited to 2-3 geographic locales. Many aspects of great gray owl ecology and biology (trophic position, aerial requirements, etc.) suggest some concern for persistence in the long term. However, habitat use patterns suggest that conservation of this owl is not necessarily at odds with forest land management in which conservation of biological diversity is a priority equal to commodity development.

Based on these factors, research on great gray owls should be approached as a long-term proposition without the extreme sense of urgency afforded species in peril. Broad-scale and long-term questions may be given a priority equal to that of short-term management needs. Furthermore, experimental studies designed in conjunction with National Forest System management activities should be a strong component of any research program.

Establish Research Goals

Research funded to support development of a conservation strategy for great gray owls should meet one of several broad goals: 1) Research should develop predictive models (qualitative or quantitative) to assist in evaluating management alternatives; 2) research should strive to understand the mechanisms responsible for differential breeding success and survival among habitats, differential dispersal of owls among habitats, and differences in home range characteristics; and 3) research should examine ways to place conservation of great gray owls in an ecosystem management context.

Develop Predictive Models

Conservation planning requires methods to predict the outcome of alternative management scenarios. These methods must consider complex ecological interactions and feedback loops among various components of forest ecosystems and must deal with processes at a variety of scales. Qualitative word models supported by quantitative submodels, where appropriate, would be most efficient to implement in management. These models should address stand, landscape, and watershed scale evaluations of the

impact of habitat change on either individual owl reproduction and survival, or population persistence. Because of the expense of developing comprehensive quantitative models and because management decisions require proper ranking of alternatives rather than precise enumeration of outcomes, models should be designed to rank habitat quality.

The data needed to support development of predictive models will come from a diversity of individual research projects and further reviews of existing literature. Some priorities for specific research are outlined below under Specific Research Topics. This research should be coordinated by the scientist or scientists responsible for building management-oriented models to assure that the research products support model development. Furthermore, research should be coordinated with research units involved with other forest predators, small mammals, and forest dynamics to avoid redundant efforts.

Examine Mechanisms

Resources to fund research are limited. Therefore, great gray owls, or any other species, cannot be studied in all geographic and environmental settings. Management, therefore, cannot take a reductionist approach and expect to base decisions on local knowledge. Instead, research must provide the basis for managers to use an inferential approach. Research that asks "why" can aid in extrapolating results from one setting to another. Inferences concerning owl habitat associations, small mammal abundance, etc., should be based on an understanding of patterns in certain locales and understanding the mechanisms responsible for those patterns. For instance, if great gray owls are observed to nest primarily in mature and older Douglas-fir stands in an area, the reason for that pattern should be examined. Knowledge of the mechanism will facilitate extrapolation of results to new areas. Studies directed toward understanding "why" will not yield unequivocal answers but the range of potential reasons can be reduced and aid in understanding the ecology of the species.

Use Ecosystem Management

The broad-scale persistence of great gray owls in the United States is not a short-term concern. Because of the mix of habitats used by great gray owls, management for this species should not place severe constraints on other management goals as long as nesting habitat is maintained to be well dispersed throughout the owl's range. Therefore, research

should focus on placing great gray owl management in an ecosystem context. As with boreal and flammulated owls, the ecology of great gray owls integrates many aspects of the forest system in which they occur. Therefore research that examines the dynamics of those links will provide knowledge useful in managing the system under a holistic philosophy. This research should dovetail with work on other forest owls as well as forest carnivores that are sensitive species throughout the western United States.

Specific Research Topics

Although the above discussion emphasizes a general direction for research, certain topics should receive priority in the early stages of a research program. These are topics that have received little attention in the past and would provide immediate input into management.

How do different habitat configurations at the landscape and broader scales influence the reproductive success of owl pairs and the probability of persistence for owl populations? Habitat quality at the landscape and regional scales has not been examined. Because many forest management activities influence the mosaic of habitats within watersheds, understanding the response of great gray owl populations to these activities are fundamental to conserving the species. Unfortunately, experiments at this scale are difficult because of the problems of studying multiple landscapes.

How is the survival of adult great gray owls influenced by habitat change? Great gray owls are long-lived and have relatively low effective reproduction. These characteristics fit the pattern of other species whose life history has been analyzed through demographic sensitivity analysis (Lande 1988, Caswell 1989). Analyses demonstrate that the persistence of populations like these are most sensitive to survival of adults. An understanding of changes in habitat that increase predation upon adults, reduce foraging success, or increase rates of adult dispersal will aid in evaluating population persistence under alternative management.

How can the response of great gray owl populations to habitat change be monitored efficiently? In certain circumstances managers will need to monitor the response of great gray owls to habitat change. Research must devise efficient monitoring methods. Rather than relying on broad-scale monitoring of territories as is done for some raptor species, I suggest testing methods to examine reproductive parameters and presence/absence as outlined in Hay-

ward *et al.* (1992). Methods to monitor adult survival would be especially useful.

How do the population dynamics of potential nest platforms vary with habitat structure? A nest platform is one of the few absolute requirements of great gray owls and a potential limiting factor under forest management that limits the extent of mature and older forest habitats. The availability of nest platforms likely differs among forest types (species composition) and forest ages within a forest type. Therefore forest management could be improved with knowledge of which forest stands are most likely to have nesting platforms now and in the future.

During both winter and summer, how is great gray owl foraging efficiency influenced by vegetation structure? As a species whose populations are frequently food limited, great gray owl persistence will depend in large part on whether or not the habitats in an area facilitate foraging. Knowledge of great gray owls and their prey that permits a ranking of habitats in terms of predicted foraging efficiency (dependent upon the effect of forest structure on both owl mobility and perception, and upon prey availability) would aid managers in choosing among stand management prescriptions.

This list of information needs is not complete. It is not intended as a template but as a set of ideas to stimulate discussion. A real research plan for the great gray owl, or other sensitive species, will depend upon a broader agreement of the urgency of the conservation problem, available funding, and opportunities to corroborate with scientists working on related problems.

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APPENDIX A

About The Authors

James R. Duncan obtained his B.S. Honors in Zoology from the University of Guelph in 1982, a B.Ed. from Queen's University in 1983, his M.Sc. from McGill University in 1985 for research on inbreeding and mate choice in American kestrels, and his Ph.D. in 1992 under Robert W. Nero studying great gray owls. He has authored and coauthored numerous publications on raptors and owls, including two species accounts in the A.O.U. Birds of North America series. Jim is currently writing a monograph on great gray owl ecology. Since March 1992, Jim has held the position of Coordinator and Research Zoologist with the Saskatchewan Conservation Data Centre, The Nature Conservancy. Meanwhile, he and his wife, Patricia (also a zoologist), have continued their studies on northern forest owl ecology in southeastern Manitoba and adjacent Minnesota. James currently monitors: small mammal population fluctuations, use of 140 potential great gray owl nests and boreal owl nest boxes, and winter owl irruptions and invasions. For four years, Jim has coordinated an annual nocturnal owl survey involving over 100 volunteers and covering over 600 kilometers of survey routes throughout Manitoba and adjacent Minnesota. Jim, Patricia, and their young son, Connor, welcome inquiries into their research and extend an invitation to those interested in visiting their study area.

James R. Habeck studied botany, plant ecology, and wildlife management at the University of Wisconsin, Madison where he received his B.S., M.S., and Ph.D., completing his final degree in 1959. He began teaching at the University of Montana soon after receiving his doctorate and continued in the capacity of Professor of Botany and Wildlife Biology until 1992 when his status changed to Post-retirement Professor of Organismal Biology and Ecology at the University of Montana. He continues to work as a consultant for the USDA Forest Service Research Natural Area Program and with the Northern Region's fire management program. While serving at the University of Montana he was granted Visiting Professorships in forestry and fire ecology at the University of Melbourne, Australia, and at CSIRO research center at Darwin and Perth, Australia. Jim's research interests have focused on phytosociological studies of Northern Rocky Mountain vegetation, fire ecology of old-growth pine-larch for-

ests, fire chronology, and the role of American Indians in vegetation patterns. He has devoted considerable effort to the establishment and study of Research Natural Areas leading to an award from USDA Forest Service Chief Dale Robertson for 20 years of work in this area.

Gregory D. Hayward received his master's and Ph.D. in wildlife ecology from the University of Idaho in 1983 and 1987. His graduate research first examined resource partitioning among forest owls in a wilderness setting and then focused on habitat use by boreal owls. After completing his graduate work Greg served as Visiting Assistant Professor at the University of Idaho prior to working with John Wiens at Colorado State University examining the effects of the Exxon Valdez oil spill on seabird populations and communities. His current research includes investigations of boreal owl demography and habitat use, small mammal habitat use, and arboreal lichen ecology. Greg currently holds a temporary position with the Rocky Mountain Forest and Range Experiment Station, Laramie, Wyoming.

Patricia H. Hayward received her bachelor's degree in wildlife resources from the University of Idaho in 1982. After completing her degree she examined the research program at Glacier National Park and summarized all science conducted in the park. Later she was co-principal investigator during studies of boreal owl ecology. She worked with Oz Garton exploring methods to examine the vulnerability of wilderness wildlife to recreation impacts and to study the demography of trumpeter swans in the tri-state population. Most recently she co-authored a review of the effectiveness of the endangered species recovery plans (Science 262:976-977). She currently devotes a majority of her time to her two sons Isaac and Philip, and she trains her appaloosa for jumping and dressage but volunteers with the Rocky Mountain Forest and Range Experiment Station to remain active in research.

Dennis H. Knight received his Ph.D. in plant ecology from the University of Wisconsin in 1964. After teaching two years at a university in Ecuador, he joined the faculty of the Botany Department at the University of Wyoming. He is now head of the Department there. His research has included studies

on vegetation dynamics in tropical forests as well as the forests, shrublands, and grasslands of the Rocky Mountain region. Also, he and his students have conducted detailed studies on the hydrology and nutrient cycling of Rocky Mountain conifer forests. A former president of the Ecological Society of America, Dennis currently serves on the editorial board of the journal *Ecological Applications* — a reflection of his long-term interest in applying ecological knowledge to the challenges of land management.

D. Archibald McCallum studied history at Davidson College (B.A., 1967) and biology at the University of Colorado (1974-1977). An ardent naturalist since childhood, he served as resident naturalist for the Cottonwood Gulch Foundation (Thoreau, New Mexico) 1977-1983, where he conducted annual breeding bird censuses, banded birds, and initiated population studies of flammulated owls and mountain chickadees. In 1983 he returned to academia, earning a Ph.D. with J.D. Ligon at the University of New Mexico in 1988 with a study of the social and population dynamics of mountain chickadees. Following postdoctoral work on growth-curve analysis with I. L. Brisbin at the Savannah River Ecology Lab, Arch joined the biology faculty of College of Charleston, in his native South Carolina, in 1990. His current research interests include population ecology of threatened species and vocal evolution in Paridae. McCallum, his wife Caroline, and daughter Conner live on Sullivan's Island near Charleston, South Carolina.

Penelope Morgan teaches and conducts research in landscape ecology, fire ecology, and forest ecology applied to management of wildland ecosystems. Intrigued by field ecology since high school, Penny earned her B.S. (Applied Biology--1977) and M.S. (Forest Ecology--1979) from Utah State University, and Ph.D. in Forestry Wildlife and Range Sciences (1984) from the University of Idaho. Following her graduate work she joined the faculty of the University of Arizona for 2 years before returning to Idaho as assistant professor in Forest Resources. Penny is currently developing a broad synthetic research program on the geography and implications of disturbance. Specific research includes models of the effects of timber harvest and fire management on bird habitat, ecosystem process modeling for management of whitebark pine ecosystems, and models of fire regimes at fine and coarse scales. Penny's work extends overseas with programs in Gambia, Ecuador, and Portugal. She will be the lead instructor for a course in ecosystem inventory, analysis, and as-

essment in the multi-agency/industry/university program, Continuing Education in Ecosystem Management. Penny has lived all her life in the Rocky Mountains. Her two children, ages two and five, keep her happily occupied.

Jon Verner, a native of Laramie, Wyoming, graduated from the University of Wyoming with a B.S. in range management in 1960 and continued his studies in biology at the University of Southern Colorado. After his discharge from the U. S. Army in 1963, Jon began his Forest Service career on the Medicine Bow National Forest. Since then Jon served as forest and district wildlife biologist on the San Isabel, Nebraska, Rio Grande, and Pike/San Isabel National Forests. In the past 5 years, Jon held several special assignments for the Rocky Mountain Region including leader of both the Mexican spotted owl center of excellence and the forest owl conservation assessment. In 1993 he was reassigned to the Rocky Mountain Regional Office to facilitate his role in leading the owl programs.



MAP 2a (addendum to Map 2) BOREAL OWL LOCATIONS AND DISTRIBUTION OF ASSOCIATED VEGETATIVE ECOSYSTEMS IN THE UNITED STATES, 1993

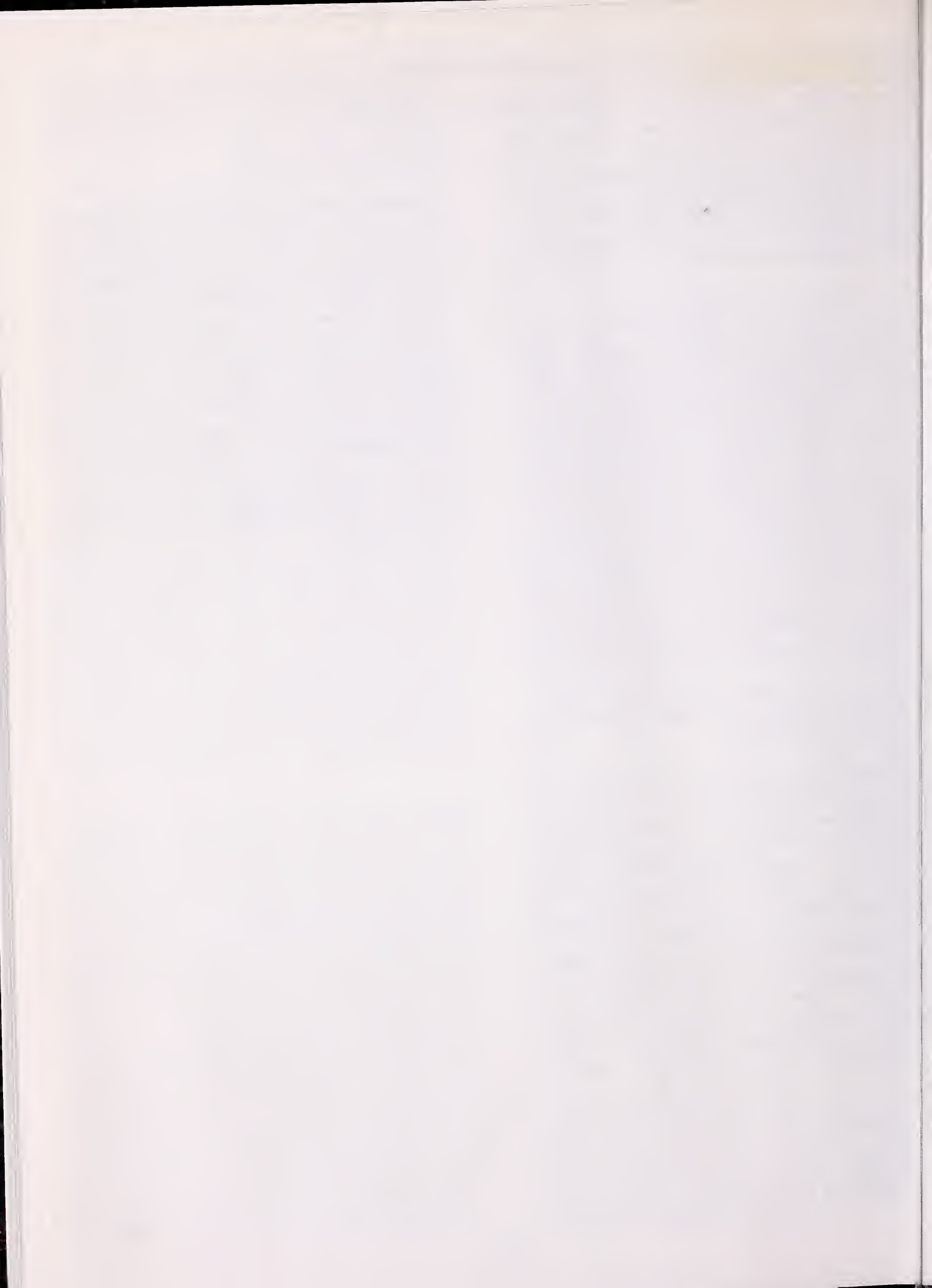
This map supplements Map 2 in: Hayward, G.D. and J. Verner, tech. eds., *Flammulated, Boreal, and Great Gray Owls in the United States: A Technical Conservation Assessment*, Gen. Tech. Rep. RM-253, Fort Collins, Colorado, U.S. Department of Agriculture, Forest Service, Rocky Mountain Forest and Range Experiment Station, 1994, 214 p., 3 maps. Boreal owl locations for Alaska were inadvertently omitted during printing of Map 2.





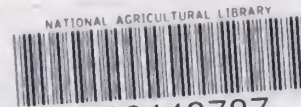






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Rocky
Mountains



Southwest



Great
Plains

U.S. Department of Agriculture
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Rocky Mountain Forest and Range Experiment Station

The Rocky Mountain Station is one of eight regional experiment stations, plus the Forest Products Laboratory and the Washington Office Staff, that make up the Forest Service research organization.

RESEARCH FOCUS

Research programs at the Rocky Mountain Station are coordinated with area universities and with other institutions. Many studies are conducted on a cooperative basis to accelerate solutions to problems involving range, water, wildlife and fish habitat, human and community development, timber, recreation, protection, and multiresource evaluation.

RESEARCH LOCATIONS

Research Work Units of the Rocky Mountain Station are operated in cooperation with universities in the following cities:

Albuquerque, New Mexico
Flagstaff, Arizona
Fort Collins, Colorado*
Laramie, Wyoming
Lincoln, Nebraska
Rapid City, South Dakota

*Station Headquarters: 240 W. Prospect Rd., Fort Collins, CO 80526